RETINAL RECEPTOR ORIENTATION IN AMBLYOPIC AND NONAMBLYOPIC EYES ASSESSED AT SEVERAL RETINAL LOCATIONS USING THE PSYCHOPHYSICAL STILES-CRAWFORD FUNCTION

By

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TABLE OF CONTENTS

		Page
AKNOWLEDGMENTS		ii
ABSTRACT		viii
CHAPTER I:	INTRODUCTION	1
CHAPTER II:	THE STILES-CRAWFORD EFFECTS	5
	Description of the Stiles-Crawford Effect	5
	Techniques of Measurement	8
	Psychophysics	8
	Objective Measures	12
	Summary and Comparison	15
	Basic Experimental Data	15
	Retinal Illuminance/Photopic vs. Scotopic Adaptation	15
	Comparisons Between Different Retinal Locations	17
	Wavelength and Absorption of Ocular Media	21
	Factors Influencing the Stiles-Crawford Effect	26
	Additivity of the Stiles-Crawford Effect within the Pupil	29
	The Stiles-Crawford Effect in Visual Pathology	31
	The Transient Stiles-Crawford Effect and Directional Light Adaptation	35
	Stiles-Crawford-like Effects in Infra-human Species	38
	Theory	42
	The Stiles-Crawford Effect of the Second Kind (SCE II)	47
	Basic Experimental Data	47
	The Stiles-Crawford Effect of the Second Kind in Anomalous Vision	51
	Stiles-Crawford Effect of the Second Kind: Theory	53
	Significance of the Stiles-Crawford Effect	54

		Page
CHAPTER III:	A BRIEF REVIEW OF FUNCTIONAL AMBLYOPIA AND OF STILES-CRAWFORD FUNCTION MEASUREMENTS IN AMBLYOPIC EYES	62
CHAPTER IV:	DEFINITION OF THE PROBLEM	72
CHAPTER V:	OBSERVERS AND EVALUATION.	76
	Observers	76
	Evaluation.	76
	History	77
	Visual Acuities	77
	Refractive Status	78
	Strabismus/Binocularity/Motility Examination.	78
	Tension and Slit Lamp, Ophthalmoscope Examination.	83
	Selection Criterion	83
CHAPTER VI:	APPARATUS AND PROCEDURES.	85
	SCE Apparatus and Testing Procedures. . .	85
	Interferometric Resolution Testing Apparatus and Procedures	94
CHAPTER VII:	RESULTS	104
	Stiles-Crawford Effect (SCE) Function Peak Locations	104
	Control Observers	104
	Amblyopic Observers	106
	Within Eye Comparisons of Peak Locations.	120
	Directionality of SCE Functions	121
	SCE Function Measurements for Observer PMC.	129
	SCE Function Peak Locations	129
	SCE Function Directionality	137
	Other Measurements Obtained on Observer PMC	138
	SCE Function Results for Observer JEC . .	145
	Visual Resolution Thresholds.	152
	Control and Amblyopic Observers . . .	152
	Resolution Thresholds for Observer JEC.	166
	Visual Resolution Thresholds at the Locus of Fixation and at the Position of the Entoptic Fovea	169

Page

CHAPTER VIII: DISCUSSION. 173
Patterns of Inferred Retinal Receptor Alignment. 173
Inferred Retinal Receptor Alignment in Observer PMC. 176
Central and Peripheral SCE Function Directionality 180
The Relationship Between Inferred Retinal Receptor Orientation and Amblyopia in the Present Sample of Amblyopic Eyes . . 181
Inferred Receptor Orientation and Visual Resolution Thresholds. 184
Visual Resolution Measurements in Amblyopic Eyes 185

CHAPTER IX: CONCLUSIONS 189

APPENDIX A: RESULTS OF CLINICAL MEASUREMENTS FOR AMBLYOPIC OBSERVERS 192

APPENDIX B: RESULTS OF CLINICAL MEASUREMENTS FOR CONTROL OBSERVERS AND FOR JEC 200

APPENDIX C: ESTIMATED SCE FUNCTION PEAK LOCATIONS . . 205
Key 204

APPENDIX D: ESTIMATED SCE FUNCTION DIRECTIONALITY . . 227

REFERENCES 245

BIOGRAPHICAL SKETCH 259

Abstract of Dissertation Presented to the
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RETINAL RECEPTOR ORIENTATION IN AMBLYOPIC AND NONAMBLYOPIC EYES ASSESSED AT SEVERAL RETINAL LOCATIONS USING THE PSYCHOPHYSICAL STILES-CRAWFORD FUNCTION

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Retinal photoreceptor orientational tendencies were assessed within both eyes of samples of control and selected functional amblyopic observers, using the psychophysical photopic Stiles-Crawford effect (SCE) function as an indicator. SCE function determinations were made at visual field testing locations spanning 30° of the horizontal meridian of the visual field.

One aim of this research was to help define the role of possible receptor alignment anomalies as a potential contributing factor to the visual resolution deficits within amblyopic eyes. A second aim of these studies was to identify individuals having anomalous patterns of inferred retinal orientation and to characterize the nature and extent of these anomalies. The nature of disturbed retinal receptor alignment within such eyes can provide information about the characteristics of hypothesized retinal photoreceptor alignment mechanisms within normal eyes.

In order to define the extent of visual resolution deficits in the sample of amblyopic eyes tested, resolution thresholds for flashed grating targets, formed by two beam interference, were determined at several of the visual field locations at which SCE function determinations were made.

The SCE function peak locations for the range of visual field locations tested were found to cluster within a subregion of the pupil for all but one of the eyes tested. Hence, in confirmation of previous such studies, retinal receptors within these eyes are presumed to tend to align toward the exit pupil of the eye.

The single exception to this generalization was found for the nonamblyopic eye of one of the amblyopic observers. Within this eye, SCE function peak locations, estimated across 45° of the horizontal meridian of the visual field and 15° of the vertical field, indicated that photoreceptors at these testing locations tended to align more closely toward the center of the eye than toward the exit pupil. Photopic increment and dark adaptometric thresholds, determined at peripheral visual field locations, were found to be elevated within this eye, consistent with predictions based upon the SCE function results. Preliminary electroretinographic results indicated disturbances in the late components of flash initiated electroretinograms in this eye. This eye represents a possibly unique opportunity to understand the mechanisms and consequences for vision of retinal photoreceptor alignment in humans.

Within the sample of amblyopic eyes tested, inferred retinal receptor alignment did not markedly differ from the pattern found within control eyes, either at foveal or other tested visual field locations. Thus, within this sample of amblyopic eyes, visual resolution deficits seemed not to be related to retinal photoreceptor alignment anomalies.

A nonamblyopic observer was identified, having a displaced foveal SCE function peak in one eye and a more nearly centered SCE function peak in the second eye. Foveal visual resolution results for this observer revealed modestly increased resolution thresholds for low photopic luminance level targets within the eye having the displaced SCE function peak and no apparent differences for higher photopic luminance targets. These data suggest that the modest amount of foveal receptor tilt present in this eye has only a slight effect upon visual resolution.

Within four of the sample of five amblyopes tested, resolution thresholds within the amblyopic eyes were found to be poorer than those of the corresponding nonamblyopic eyes at both central and near peripheral (to 10° visual field) locations. Additionally, in two amblyopic observers having eccentric monocular fixation positions, best resolution thresholds were determined at the region corresponding to the location of the fovea, rather than at the locus of eccentric fixation.

The results of this dissertation have implications for both the nature of retinal photoreceptor alignment mechanisms and for the understanding of functional amblyopia.

CHAPTER I
INTRODUCTION

This dissertation is an attempt to define the extent to which possible anomalies at one level of the human visual system contribute to the pathophysiology of functional amblyopia.

Functional amblyopia is characterized by a diminished visual acuity, usually in one eye only, which is not resolved by optimal refractive correction. Gross indications of pathology are either absent or are of insufficient magnitude to account for the acuity loss.*

A rather extensive body of evidence indicates that the psychophysical Stiles-Crawford effect (SCE) function reflects the orientational properties of retinal photoreceptor groups. This evidence, as well as a fuller description of the SCE, is presented in Chapter II. Since grossly maloriented receptors have been observed to degrade retinal resolution capability (see Chapter II), a direct relationship is indicated

*For the purposes of this argument, any ocular or systemic condition which impairs vision and is localizable in its effect is deemed to be pathological. Thus, for example, opacification of the lens, which may simply be related to the ageing process, and various avitaminoses which impair photopigment production, transport and/or regeneration, are here considered to be pathologies.

between possible photoreceptor orientation anomalies and at least a modest amount of visual resolution impairment.

As the major portion of this dissertation research, the orientational tendency of groups of photoreceptors at a number of retinal test locations within amblyopic eyes, for the most part having only limited visual loss, and non-amblyopic eyes has been inferred from SCE function determinations. In order that inferred receptor alignment might be compared with visual resolution capability in the same eyes, minimum angles of resolution for an interferometrically formed grating target were measured at a number of locations at which SCE function measurements were carried out.

This research was approached from a second and complementary point of view as well. In the eyes of all species so far examined histologically, photoreceptors at all regions of the retina tend to align toward the anterior part of the eye and presumably toward the pupil, which is the source of relevant visual stimuli. This analysis has been extended to human observers utilizing the SCE function as an indicator of retinal receptor orientation. The results from the eyes of normal human observers indicate that the photoreceptors tend to align toward a region near the center of the pupil, for test locations as far as 35° in the peripheral visual field. Additionally, a limited number of cases have been documented, in which the SCE function, and hence presumably receptor alignment, was disturbed during the active phase of retinal pathology but subsequently recovered in conjunction

with remission of the pathological condition. All of these data are more fully reviewed in Chapter II. Taken together, they strongly indicate that an active process governs photoreceptor orientation. The mechanism or mechanisms by which receptors obtain and maintain their alignment with respect to the pupil remain to be clarified.

Previous SCE function measurements in amblyopic eyes (reviewed in Chapter III) indicate that, in some cases, receptor alignment at the locus of fixation is disturbed. Such disturbances might reflect a general alignment tendency for all receptors within such eyes toward an anomalous alignment centrum displaced from the exit pupil center. Alternatively, photoreceptor alignment at more peripheral retinal locations might show a tendency for orientation toward the pupil center. In either case, measurements which assess photoreceptor alignment within these amblyopic eyes at a number of retinal locations would presumably give information concerning the nature of the mechanism or mechanisms by which receptors maintain their alignment. For example, one might distinguish whether alignment is governed by retina-wide (global) or by more local control mechanisms. Thus, the nature of receptor alignment in amblyopic eyes was approached with the idea of elucidating a possible model in which normal receptor alignment mechanisms might be studied.

As a part of this investigation, a unique individual was identified. Photoreceptor orientation within one eye only of this individual was determined to be directed more closely

toward the center of the retinal sphere than toward the eye pupil. Studies of this individual are presented in Chapter VII. The identification of this individual has important implications relative to mechanisms subserving receptor alignment and, moreover, promises to permit the consequences for vision of anterior (pupil) pointing of photoreceptors to be assessed.

Thus, this study is an attempt to characterize possible photoreceptor alignment anomalies within amblyopic eyes with relation to the visual loss sustained in these eyes and, moreover, to evaluate the implications of these findings for hypothesized receptor alignment mechanisms within normal eyes.

CHAPTER II
THE STILES-CRAWFORD EFFECTS

Description of the Stiles-Crawford Effect

The discovery of the Stiles-Crawford effect arose from an attempt to determine pupil size from visual photometric matching data. The technique employed by Stiles and Crawford assumed that a homogeneous beam of light, limited by the pupil, should change in apparent brightness exactly with the area of the pupillary opening. By making a visual brightness match between such a homogeneous beam, for which the pupil forms the aperture stop, and a second beam which passes through the pupil in sufficiently small cross section so that retinal illuminance is unaffected by the pupil size, one ought to be able to determine pupil area, and hence its diameter, from the luminance ratio of the two beams at the subjective match point. When Stiles and Crawford (1933) performed this experiment, calculated pupil sizes consistently deviated, in the direction of underestimation, from reported objective (photographic) results. By then employing two beams, both of which entered the artificially dilated pupil in small cross section (using Maxwellian view), and by making brightness matches when these beams were separated by varying distances in the pupil (one held at the pupil center for

convenience), it was found, under conditions of foveal viewing, that a beam entering the periphery of the pupil had to have a luminance of from 5 to 10 times that of a beam entering the pupil center to provide the same subjective brightness.* That is, a beam passing through the periphery of the pupil was judged considerably less bright than a physically equal beam entering at the center.

Stiles and Crawford plotted the parameter η, defined as the ratio of the luminance of the standard beam (at the pupil center) to that of the displaced beam at the photometric match point, against the position of entry of the displaced beam in the pupil. The resulting curves were essentially symmetrical about a maximum value at or near the pupil center and decreased monotonically to the pupil margins.

Stiles (1937) empirically fit the psychophysical retinal directional sensitivity function, or SCE function, with the equation

$$\log \eta = \log \eta \text{ max} - \rho r^2$$

---

*Throughout this discussion luminance will be used to refer to the physical properties of the light stimulus, as corrected for the spectral response characteristics of a standard observer, whereas brightness will be reserved for the subjective impression occasioned by the stimulus. Thus, the Stiles-Crawford effect represents a situation in which luminance and brightness, as defined here, are dissociated, in that a source of constant luminance is judged to change in brightness depending upon the region of the pupil through which light from the source enters the eye. Some authors have attempted to incorporate a correction for the SCE into the definition of retinal illuminance (Wyszecki and Stiles, 1967; LeGrand, 1968, see below).

The parameter η is as defined above and η max is the value of η at the function maximum. Distance within the entrance pupil from the function peak in mm is represented as r. The shape parameter, ρ, provides an index of the directionality, or the spread, represented by the function. Enoch and Bedell (1978) have suggested the use of the half sensitivity half width, i.e., the distance within the entrance pupil, in mm, from the SCE function peak to the position at which η falls to one-half of η max, as a more readily interpretable indicator of SCE function directionality.

Stiles and Crawford (1933) calculated the differential light absorption which would occur within the eye media for beams entering the pupil centrally and peripherally, based on published data for ox eye media. Since the calculated difference in absorption was small, they concluded that the effect they described was not preretinal in origin. Craik (1940) determined that preretinal absorption in cat and frog eyes was insufficient to account for the SCE; however, Stiles-Crawford-like effects had not been measured for either animal. Good evidence that the SCE is, in fact, retinal in origin derives from Crawford's (1937) discovery that the phenomenon is greatly reduced in going from photopic to scotopic vision. Presumably the change in adaptation state represents a change of the retinal receptor type mediating brightness rather than of preretinal absorption. Moreover, the SCE has been shown to be greatly altered, and in some cases to subsequently recover, in some retinal and pigmented epithelial pathologies which do not alter preretinal absorption (see below).

The underlying basis of the SCE is currently thought to be the differential sensitivity of the photoreceptors and associated morphological elements to light striking them at different angles; one mm in the pupil corresponding to nearly 2.5° of angle at the fovea (O'Brien, 1946). Light entering the receptors parallel to their long axes is presumably the most effective for producing excitation. Hence, the SCE function apparently samples the orientational properties of groups of retinal photoreceptors.

Techniques of Measurement

Psychophysics

In their original measurements, Stiles and Crawford employed both direct photometric matching and flicker photometry, both techniques giving essentially the same results. Flicker matches were reported to have the advantage of reducing the disturbing effects of ocular aberrations for beams displaced toward the periphery of the pupil and hence imaged along an off-axis optical path within the eye. Enoch (1958), who also compared direct matching and flicker photometric techniques for Stiles-Crawford effect curve determinations, found that blurring introduced by the peripheral pupil path of the displaced beam caused a brightness decrement for beams passing eccentrically in the pupil in addition to that produced by the SCE itself. Flicker photometrically measured SCE curves were found to be less sensitive to optical blur. Additionally, when SCE functions were determined with narrow

band spectral stimuli, rather than with white light, the effect of chromatic aberration upon beams which enter peripherally in the pupil, and which disturbs both flicker and direct matching judgments, was minimized.

Wright and Nelson (1936) were among the first authors to confirm the basic SCE phenomenon, using Wright's binocular colorimeter to obtain measurements. A field produced by a moveable beam entering one pupil was matched to a closely apposed field seen by the other eye and fixed in its entry position at the pupil center.

Crawford (1937) measured SCE functions by finding the incremental threshold for a small test field. The test beam's entry position in the pupil was displaced for successive threshold determinations whereas the background beam always entered at the pupil center. The SCE curves determined by the increment threshold procedure were comparable in all respects to those determined by direct photometric matching. Some of Crawford's measurements were made with the background field extinguished, i.e., as the absolute threshold for the test beam as a function of its pupillary entry position. For test fields confined to the foveal region, absolute and increment threshold determinations of the SCE gave similar results. Crawford's experiments indicated that the foveal SCE is relatively unaffected by the condition of light adaptation (but see below) and, moreover, provided the empirical justification for the use of sensitive threshold techniques in SCE measurements. [At about the same time, Goodeve (1936),

who was investigating the visibility of stimuli in the far red region of the spectrum, also utilized a threshold procedure to indicate the existence of an SCE at wavelengths of about 830 nm.]

Flamant and Stiles (1948) used the increment threshold technique to determine peripheral photopic and scotopic SCE functions. In the procedure they adopted, the test beam was fixed at the pupil center and the surround field beam was displaced across the pupil. This modification of the earlier increment threshold technique has the advantage that the larger surround field, rather than the smaller test field, is subjected to the off-axis optical aberrations of the eye. Thresholds for small fields are highly dependent upon blur, as evidenced by the use of stigmatoscopy for visual refraction (Ames and Glidden, 1928), whereas larger fields are less so (Ogle, 1961a, b). Additionally, since the surround field beam is displaced across the pupil, its image undergoes whatever shifts of position on the retina may accrue from spherical and other aberrations, instead of the test field's image. This assures that thresholds are always determined for the same retinal locus with respect to a stationary fixation target.

The particular increment threshold technique employed by Flamant and Stiles (and others) measures the SCE indirectly, however. What is actually determined is the threshold change in the incremental field produced by the change of brightness of the surround field due to the SCE. Fortunately,

insofar as the Weber relation holds, i.e., $\Delta L/L$ = constant, which is over a considerable range of luminances in normal observers, the change in the surround field brightness, in logarithmic units, is accompanied by an equal change in the log luminance of the increment at threshold:

$$\Delta L/L = \text{constant (Weber relation)}$$

$$\text{thus } \Delta Lo/Lo = \Delta Lx/Lx$$

where ΔL and L are the luminances of the incremental and surround fields, and the subscripts refer to the reference (o) and displaced (x) beams.

Therefore, $\log (\Delta Lo) - \log (Lo) = \log (\Delta Lx) - \log (Lx)$

hence, $\log (Lo) - \log (Lx) = \log (\Delta Lo) - \log (\Delta Lx)$

(or change in log surround = change in log increment).

Moreover, since

$$\eta = Lx/Lo$$

$$\text{and } \log \eta = \log (Lx) - \log (Lo)$$

$\log \eta$ may be plotted as the differences in log increment threshold values between the displaced and reference beams. Thus, over the Weber range of the increment threshold curve, measurement of changes in increment threshold is equivalent to measurement of changes in effective background luminance. It is apparent, however, that for regions of the increment threshold curve other than the Weber portion, increment threshold changes are not equal to changes in the effective luminance of the surround field; hence, increment thresholds as a function of the pupil entry position of the background beam do not adequately represent the SCE.

In practice, an increment threshold function is obtained with the entry position of the background beam held fixed in order to determine a background field luminance for which a valid SCE function may be obtained.

Blank et al. (1975) described a rapid method for determining the location of the peak of the SCE function (also see Enoch, 1959a). Two beams are made to enter the pupil at a fixed separation (2 mm in practice); light from each beam forms one-half of a bipartite photometric field. The pupillary entry positions of the two beams, which move in tandem, are adjusted to give a photometric match. If symmetry of the SCE function about its peak is assumed or has previously been determined, then at the match point the entry positions of the two beams in the pupil straddle the position of the SCE peak in the tested pupillary meridian. In principle, this peak finding technique might be modified to generate entire SCE functions as well.

Objective Measures

In 1937, Crawford, using a subjective psychophysical technique, measured the recovery of visual sensitivity in the dark following a light preadaptation mediated by a beam either entering at the pupil center or near its margin. As expected, higher thresholds were evident during the early phase of the recovery of sensitivity (the cone portion) when the adaptating stimulus entered at the pupil center, i.e., close to the peak of the SCE function.

Presumably, the recovery of visual sensitivity after exposure to bright light depends in large part upon the regeneration of bleached pigment (Rushton, 1972). Crawford measured the recovery of sensitivity in time, from which the pigment bleaching effectiveness of adapting beams entering the pupil centrally or eccentrically could be inferred. With the development of fundus reflectometry techniques, by which retinal photopigment could be measured directly before and after exposure to pigment bleaching adapting lights, pigment bleaching efficacy could be directly measured as a function of the pupil entry position of the adapting beam. [Goldmann (1942) performed an experiment, similar in principle, which anticipated fundus reflectometry. He noted ophthalmoscopically that retinal images formed by central and peripheral pupillary beams were unequally bright when the observer whose retina he was observing had photometrically matched the two fields.] Thus, Ripps and Weale (1964) determined that the relative efficacy of monochromatic lights in bleaching foveal photopigment when these entered either at the pupil center or 3 mm displaced was comparable to the relative efficacy of these lights in producing brightness. Coble and Rushton (1971) found adapting light intensities which produced equal photopigment bleaching for entry positions spaced across the eye pupil. The obtained "equal bleaching" function was in excellent agreement with a psychophysically determined SCE function for the same observer.

Spring and Stiles (1948) changed the pupil entry position of a large (52°) Maxwellian view adapting field and measured the consensual pupillary reflex in the contralateral eye. They observed a relative dilation of the contralateral eye when the adapting beam entered peripherally in the pupil as compared with central entry; however, the effect was considerably less than was expected on the basis of the psychophysically determined SCE. It seems probable, however, that the large white field used by these investigators favored peripheral rods rather than central cones, in which case a much reduced SCE would be expected (see below). Alpern and Benson (1953) repeated the Spring and Stiles study using a centrally viewed 1° red adapting field in order to favor cone vision. Under these conditions, a considerable change in contralateral pupil diameter was recorded, consistent with the psychophysically determined SCE, when the entry position of the adapting light was displaced in the ipsilateral pupil.

Both Armington (1967) and Sternheim and Riggs (1968) employed electrophysiological methods to determine SCE functions in human observers. In both cases constant luminance but pattern modulated stimuli were used to evoke electroretinographic (ERG) responses favoring cone activity. ERG and psychophysically determined SCE functions were highly similar. Sternheim and Riggs also measured fast flicker (25 Hz) ERGs for different pupil entry positions of a homogeneous stimulating beam which yielded a function quite like the psychophysical SCE as well. Slow flicker (4 Hz) ERGs

showed much less amplitude change as pupil entry position was altered; presumably scotopic activity was preferentially tapped with this procedure.

Summary and Comparison

The SCE is a remarkably robust phenomenon in terms of its insensitivity to the technique by which it is measured. Thus, psychophysical, electrophysiological and other objective techniques all yield very similar functions, although the variability of data and potential artifacts encountered with some techniques make them less attractive than others. [The techniques described here by no means exhaust the possible alternatives. For example, at the suggestion of Dr. Michael Halasz, of the National Eye Institute, an SCE function has been successfully determined using a suprathreshold magnitude estimation direct scaling paradigm. Stiles (1959), Westheimer (1968), and Heath and Walraven (1970) all describe procedures by which the SCE can be visualized entoptically. Local variations in the SCE may also be seen entoptically (see below.)] In general, psychophysical threshold measures show the least variability; when coupled with criterion independent (signal detection) paradigms a remarkable degree of sensitivity can be achieved.

Basic Experimental Data

Retinal Illuminance/Photopic vs. Scotopic Adaptation

Crawford's (1937) study indicated that the foveal SCE function was essentially independent of the background

luminance. Both Stiles (1939) and Crawford (1937) showed a similar independence of background luminance for the extrafoveal SCE provided the level was relatively high (greater than ca. 1.2 log photopic td at 5°). At low background intensities or at absolute threshold, extrafoveal SCE functions were reported to be much more nearly flat (Crawford, 1937; Stiles, 1939; Flamant and Stiles, 1948), indicating that in scotopic vision, brightness is much less dependent upon entry position of the beam in the pupil. Using a sensitive signal detection psychophysical procedure, vanLoo and Enoch (1975) definitively demonstrated the existence of a scotopic SCE on the order of 0.2 - 0.3 log units which had been previously hinted at in Stiles (1937) data and occasionally in subjects whose SCE functions were decentered in the pupil (Flamant and Stiles, 1948; Daw and Enoch, 1973; Bonds and MacLeod, 1978). When correction was made for the differential path lengths of central and peripheral beams through absorbing lens pigment (see below), the magnitude of the scotopic effect was found to be quite similar at all wavelengths tested. Moreover, both photopic and scotopic SCE functions taken at the same retinal locus had common axes of symmetry with reference to the pupil. This finding is highly significant in terms of the retinal receptor orientation properties which the SCE apparently reflects.

In the mesopic range, the SCE makes a gradual transition between the small scotopic effect and the larger photopic effect. This so-called "rising-sun" phenomenon was first reported by Crawford (1937).

At very high photopic levels, the magnitude of the SCE at the fovea increases, i.e., there is more difference in brightness between beams passing through the center and periphery of the pupil (Stiles, 1937; Miller, 1964). Walraven (1966) has also confirmed this effect for midspectral monochromatic lights and proposed that it may be due to cone pigment bleaching (see below). In an often cited article LeGrand (1948) reported that the peak of the SCE curve shifted with respect to the position of the corneal reflex (produced by the photometric field) in an orderly fashion as the testing luminance was changed. This intriguing finding is not replicated in either Crawford's (1937) or Miller's (1964) data. LeGrand's results may reflect a change in position of the corneal reflex with luminance changes, due perhaps to altered fixation (Simon, 1904), rather than of the position of the SCE peak in the pupil.

Comparisons Between Different Retinal Locations

Westheimer (1967) argued that if the SCE reflected retinal photoreceptor optical properties, and if these were physical optical rather than geometrical optical in character, due to the small size of receptor apertures (Toraldo di Francia, 1949), then foveal and extrafoveal photopic SCE functions might be expected to differ, reflecting anatomical differences between foveal and extrafoveal cones. In fact, he found that the foveal SCE was of lesser magnitude than that measured 3-3/4° parafoveally. Similar results can also be

seen in the data of Vos and Huigen (1962) taken at 0° and 4°, although these authors failed to comment on this finding. Stiles' (1939) results also indicate a larger SCE parafoveally (5°) than foveally for long wavelength stimuli; the same relationship is not seen in his short wavelength data (but see below). Enoch and Hope (1973) measured SCE functions for orange test and surround fields at 0°, 2°, 3-3/4° and 10° and found that the change in magnitude of the SCE occurred between 0° and 2° with little change thereafter out to 10°. Recently, Bedell and Enoch (1978) determined that the SCE at 35° is similar in magnitude to that at the fovea.

Histological investigations in many species have shown that photoreceptors do not point toward the center of the eye but rather toward some anterior location, presumably within the pupil (Laties et al., 1968; Laties, 1969; Laties and Enoch, 1971; Enoch, 1972; Enoch and Horowitz, 1974; Baylor and Fettiplace, 1975). Webb has drawn similar conclusions based upon the X-ray diffraction patterns produced by photoreceptors in intact eyes (Webb, 1972; 1977). Thus, only in the vicinity of the posterior pole are receptors perpendicularly aligned with respect to the underlying pigment epithelium substrate.

Inasmuch as the SCE represents the orienting properties of the photoreceptors (Enoch and Laties, 1971), one would expect that peaks of SCE functions measured at different retinal loci would mirror these histological findings, i.e., SCE peaks should maintain an approximately constant relation

to the pupil center. In the earliest study in which the SCE was determined over a considerable range of retinal locations, Aguilar and Plaza (1954) found that SCE peaks up to 37° from the fovea remained within the dilated entrance pupil. Enoch and Hope (1972a) carefully measured SCE functions from 5° in the temporal visual field, approximately the posterior pole, to 20° in the nasal visual field. Their findings were that both horizontal and vertical traverses of the pupil yielded SCE peaks clustered about a point, slightly different for each of their three observers but for each near the center of the entrance pupil of the eye. They confirmed these results for three more observers at loci between 0° and 10° in another study (Enoch and Hope, 1973). Bedell and Enoch (1978) extended this analysis to 35° in the temporal peripheral field and found that receptor alignment within the pupil is maintained. Because the optic disc is interposed between this peripheral region and the fovea, forces which act on the retina, such as occur in accommodation and during rapid eye movements (see below) will have somewhat different effects in these two areas. Thus, receptor alignment toward a region within the eye pupil on both temporal and nasal sides of the optic disc is quite remarkable.

VanLoo and Enoch (1975) found that photopic and scotopic SCE functions had a common axis of symmetry when measured at 6° in the nasal visual field. Results of Bedell and Enoch (1978) for one observer at 35° in the nasal retina are also indicative of common alignment of photopic and scotopic

receptors (see also Flamant and Stiles, 1948; Daw and Enoch, 1973; Bonds and MacLeod, 1978).

Given the consistency of their results, Enoch and Hope (1972b) sought to determine whether the foveal SCE peak better aligned to the center of the dilated or constricted pupil, since the pupil center shifts slightly nasally from complete dilation to complete constriction (Gullstrand, 1962; Enoch and Hope, 1972b). Moreover, normal SCE functions have a slight bias toward peaking on the nasal side of the dilated pupil center (e.g., Dunnewold, 1964). Enoch and Hope measured SCE curves with respect to the corneal reflex, since the pupil center obviously could not be used. They employed a "peak finding" technique, in which observers adjusted two equal luminance beams having a fixed separation in the entrance pupil, to that position of pupil entry which rendered both fields equally bright. Although for two of three observers SCE peaks were nearer to the constricted than to the dilated pupil center, the result must be taken to be inconclusive.

While the overall pattern of receptor pointing, as inferred from the SCE , is remarkably constant across at least a considerable region of the retina, there is apparently some degree of variability, as would be expected in any biological system, in the alignment of groups of neighboring receptors. This was first recognized by O'Brien (1950) who constructed an aperture which corrected for the photopic SCE but saw residual bright and dark patches in what was

expected to be a uniform field. Brighter and darker regions shifted with respect to one another as the entry position of the compensated beam in the pupil was altered. The effect rapidly faded when the beam was not moved, presumably due to image stabilization. The same phenomenon has been reported by Enoch (1967) and by Heath and Walraven (1970) for short flashes. Enoch et al. (1978) have observed that a similar, if somewhat more difficult to observe, effect also occurs in scotopic vision, apparently reflecting local variations in orientation of groups of rods. All observations to date have been qualitative only.

Heath and Walraven (1970) proposed that in the central 4° of the retina, receptors are parallel rather than pointing toward a common point in the eye pupil. Their evidence consists of slight shifts of SCE function peaks measured in this region. Since the shifts involved are rather small and since these results have not been replicated (Enoch and Hope, 1972b), this proposed departure from anterior pointing of photoreceptors must be regarded as questionable.

Wavelength and Absorption of Ocular Media

Stiles (1937) reported that the magnitude of the foveal SCE changed systematically with the wavelength of the test stimulus. He found the smallest SCE in the green region and larger effects at both ends of an equal luminance spectrum. In later work (Stiles, 1939), he confirmed this general wavelength dependence; however, he measured a smaller

SCE at all wavelengths using different measurement techniques. Both sets of measurements were on Stiles' own eye, which during this period also evidenced a shift in the peak of the SCE (see below).

Foveal SCE data as a function of wavelength have also been published by Enoch and Stiles (1961) for two subjects, as raw data only, also for two observers, by Safir and Hyams (1969), and for one observer by Wijngaard and van Kruysbergen (1975). In all cases, a larger SCE is observed for long and short wavelength than for mid-sprectral monochromatic targets.

In 1939, Stiles also measured the wavelength dependence of the photopic SCE for parafoveal targets. Here the SCE was largest at the red end of the spectrum, falling to a rather constant (non-zero) value in the green and blue regions. This experiment has apparently never been repeated. It is curious that the wavelength dependence of the SCE for the foveal and parafoveal photopic retina should differ. Although the parafoveal curves are not at all scotopic in appearance, a possible rod contribution at the more eccentric pupil entry positions needs to be considered. This is, in fact, suggested by discrepancies between SCE functions determined by increment thresholds in which test and surround fields were of the same wavelength and functions determined with test and surround of different wavelengths. (Compare Stiles, 1939, Fig. 13 with Fig. 20, 23.) It can thus be said that the wavelength dependence of the photopic SCE outside of the fovea is an open question. On the other hand,

the magnitude of the scotopic SCE seems to be less dependent on wavelength, after correction has been made for absorption by the ocular media (Flamant and Stiles, 1948; VanLoo and Enoch, 1975).

Returning to the foveal data, the function of magnitude of the SCE vs. wavelength has been suggested to represent a composite of the somewhat different directional sensitivities of three cone types posited for trichromatic vision (Stiles, 1937, 1939; Enoch and Stiles, 1961; Walraven and Bouman, 1960; Safir et al., 1971). Stiles (1939) approached this problem by determining increment threshold functions for a variety of test field, surround field wavelength combinations and either central or peripheral pupil entry of the test beam. For some combinations of test and surround wavelengths, the difference between increment threshold curves for central and peripheral pupil entry of the test beam changed more or less abruptly as a function of the background luminance, indicating a change in the directional sensitivity of the detecting mechanism. Stiles interpreted these data in terms of three cone mechanisms, the blue cones being more directionally sensitive than either the red or green cones, and the green cones slightly more so than the red cones for wavelengths under 620 nm.

Enoch and Stiles (1961) calculated the directional sensitivities of three cone types based on color matching functions for central and peripheral pupil entry of test fields. The results indicate that all three receptor types

have directional sensitivities which change as a function of wavelength; the blue receptors were found to be more directionally sensitive than either the red or green receptors.

The effect of strong light adaptation on the magnitude of the SCE was briefly alluded to above. Stiles (1937) noted a marked increase of the SCE in midspectrum for high luminance targets. Walraven (1966) also found evidence for an increased SCE after strong light adaptation for "green" sensitive elements but not for long wavelength sensitive receptors. Additionally, he measured a recovery period for this increased SCE, with a time constant of ca. 30 sec, consistent with that of cone photochemical regeneration following bleaching. Brindley (1953) noted that the Stiles-Crawford hue change (SCE II; see below) effectively disappeared when the eye was first exposed to a bright adapting stimulus (but see also Wooten et al., 1977). Earlier, Wright (1946) had determined that the foveal luminosity curve for a Maxwellian view beam entering the pupil 3 mm from its center was most similar to the luminosity curve for a higher luminance target entering at the pupil center. Taken together, these results suggest that eccentric pupil entry and light adaptation have comparable influences on (at least midspectral) luminosity. Brindley (1953), following a proposal made by Stiles (1937), suggested that this similarity might be due to reduced effective receptor photopigment concentration in both instances; due to a partial bleaching from light adaptation and to a diminished effective absorbing path length

within the receptor in the case of oblique incidence. These ideas will be further treated below.

Corrections for ocular media. While the SCE would seem to be primarily retinal in origin, the "retinal function" is modified somewhat by differential absorption of beams passing through the center and periphery of the pupil within the eye media. The bulk of the absorption within the eye is attributable to the lens pigment which most effectively absorbs light at the short wavelength end of the spectrum. Macular pigment absorption is relatively unimportant since the path length differences involved are only about 2 per cent.

Weale (1961) corrected the magnitude of the SCE as a function of wavelength for lens absorption, assuming homogeneous pigment concentration throughout the lens. Since the path length through the lens is longer for beams passing through the center than through the periphery, the correction results in a modest increase in the magnitude of the SCE at middle and long wavelengths; at short wavelengths, the increase in the (presumed retinal) SCE is quite substantial. Weale also noted that after lens path correction, Stiles' 1939 data indicated a small SCE in scotopic vision; this effect was later measured by VanLoo and Enoch (1975).

Mellerio (1971) investigated Weale's assumption that lens pigmentation was homogeneous, finding it to be correct. His own results indicated that changes in lens absorption with age reflected increased lens thickness rather than increased pigment density. He calculated a correction for the

SCE based on his data, indicating an even larger SCE at short wavelengths than Weale.

Vos and van Os (1975) challenged the Mellerio correction for short wavelengths, arguing that he failed to account for the slight decentration of the SCE peak in the pupil generally found in normal observers. They argued that the effect of lens pigment at short wavelengths is to displace the psychophysically determined SCE peak and distort the function's shape, rather than to diminish its magnitude by as much as the Weale and Mellerio corrections suggest. It would seem that the validity of the various lens corrections could be addressed experimentally in a aphakic observer, corrected with a corneal contact lens, as suggested by Bailey (1972).

Factors Influencing the Stiles-Crawford Effect

Richards (1969) hypothesized that the rise in visual threshold which accompanies rapid eye movements, or saccades, may be due, in part, to forces acting on the retina as the result of the eye movement. In particular, he proposed that the retina might be subjected to a sheering force relative to its substrate during the rapid acceleration and deceleration phases of saccades. If such sheering occurred, it might be expected to transiently alter receptor orientation. Such an effect would presumably be reflected in the SCE, if measured directly after saccades. In fact, foveal SCE functions determined 40 msec after 5° amplitude saccades showed

a 0.6 mm shift in the peak toward the temporal edge of the pupil.

More recently, Blank et al. (1975) showed that foveal SCE function peaks shifted between one-half and one and a half mm nasally in four eyes under conditions of marked (9 D) accommodation. Marked accommodation had previously been shown to result in an advance of the retinal boundary toward the ciliary body, which had been calculated to increase retinal area by over 2 per cent (Moses, 1970; Enoch, 1973).

Ronchi (1954, 1955) reported that mydriatic agents, both a parasympathetic blocking agent, and hence cycloplegic, and a sympathomimetic, affected the magnitude of the foveal SCE. Both the direction and amount of change in the SCE (assessed as the change in $\log \eta$) depended upon the drug used and the time since instillation. Effects lasted for several hours. No influence of the drugs on the location of the SCE peak was described; however, since most of the measurements were a comparison of the relative efficacies for two points in the pupil, rather than determination of entire SCE curves, influences upon the peak cannot be discounted, and may, in fact, represent much of the described effect. It is not inconceivable that such drugs might introduce forces upon the retina which would alter the position of the SCE peak. Retinal distortion, tearing, and detachment are known, for example, to occasionally accompany the use of powerful miotic agents such as diisopropyl fluorophosphate and phospholine iodide (Lemcke and Pischel, 1966; Moses, 1970).

In 1939, Stiles reported the results of six years of SCE determinations on his own eye. During that period the peak of his foveal SCE function had shifted from 0.2 mm nasal of pupil center (Stiles and Crawford, 1933) to 0.9 mm temporal in 1939 (Stiles, 1939), giving a total shift in the horizontal meridian of just over 1 mm. Very little or no change occurred in the position of the SCE peak for a vertical pupillary traverse. Crawford's eye showed essentially no change in the position of the horizontal peak from 1933 to 1937 (Stiles, 1939). Safir et al. (1970) failed to find any horizontal shift in the SCE peaks of two observers over two years. Bedell and Enoch (1978) measured both vertical and horizontal foveal SCE functions for two observers and compared these with earlier data. In one case, no change in either peak could be detected after a lapse of five years; in the second, a 0.4 mm horizontal shift was detected over a 17 year interval. (As a point of reference, a 1 mm shift in the position of the SCE peak in the entrance pupil corresponds to a change in angle of approximately 2-1/2° at the posterior pole.)

With the exception of Stiles' eye, then, normal SCE function peak positions within the pupil are remarkably stable over time considering the stresses to which the retina is constantly exposed. In contrast, cases of active retinal pathology may show changes in the position of the SCE peak over the course of months (e.g., Campos et al.,

1978). Transient changes of the position of the SCE peak can result from forces acting upon the retina, such as accompany rapid eye movements or accommodation. It is possible that a shifting of the SCE peak over time in a normal eye may reflect the action or relaxation of such forces.

Additivity of the Stiles-Crawford Effect within the Pupil

In the paper in which Stiles and Crawford first reported the SCE, they also investigated whether the relation which described the relative brightness of beams entering at two points in the pupil also described the brightness of a beam which filled the pupil (Stiles and Crawford, 1933). They found that when they graphically integrated the data for horizontal and vertical traverses of the pupil across the entire pupillary aperture, their predictions for the apparent brightness of extended beams were good to 6 per cent or less. Since this first study others have reported slight departures from perfect additivity in one direction or the other (e.g., Ercoles et al., 1956; Ronchi, 1955; Enoch, 1958). Enoch's study demonstrated that some and perhaps most of the departures from additivity resulted from the blurring of off-axis images. He found much closer approaches to perfect additivity when blur was corrected or when brightness was determined by flicker photometry rather than direct matching. What has perhaps not been adequately appreciated is that all tests of additivity rest upon the assumption of a perfect radial symmetry of the psychophysically determined SCE

function as well as a perfect description of the SCE by the mathematical function chosen to represent the data. Clearly neither assumption is warranted.*

Drum (1975) sought to determine whether the SCE occurred for non-Maxwellian view stimuli, i.e., whether the SCE was an artifact of Maxwellian view optics, a problem which Enoch had also addressed earlier. Drum found that the SCE did occur with Fraunhofer images of his stimuli (which corresponds to normal viewing circumstances) and that the brightness of a stimulus which passed through the pupil in an annular beam was virtually exactly predicted from the average of the brightnesses of four quarter annuli.

Corrections of retinal illumination through an extended pupil for the SCE to yield an effective retinal illumination have been offered (Moon and Spencer, 1944; Wyszecki and Stiles, 1967; LeGrand, 1968). Not only do these corrections assume additivity but also a standard observer with an SCE centered in the pupil. Moreover, they are predicated upon foveal viewing, a moderate luminance and white light. It is seen that such corrections are useful as a general approximation in photometry.

Enoch and Laties (1971) addressed the question of the effect of a decentered SCE within the pupil upon perceived

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*Even if the retinal SCE were perfectly symmetric about its peak, which is not established, differential lens absorption for different optical paths would tend to distort the psychophysical function for a peak not centered in the pupil (see above).

brightness for viewing with natural pupils of various sizes. They employed an analog device (an aperture incorporating the SCE) and assumed perfect additivity. The results indicate that decentering of the SCE peak in the pupil has only a moderate effect upon "integrated brightness"; a decentered SCE more reduced "brightness" for smaller than larger pupil sizes.

The Stiles-Crawford Effect in Visual Pathology

Clearly the precise receptor alignment which is seen in careful histology, and is presumably reflected in the normal SCE, may be altered or disrupted by the action of pathological or aphysiological challenges to the retina or pigmented epithelium. Thus, Fankhauser et al. (1961) documented anomalies of the SCE in patients with retinal detachment, angiomatosis of the retina and retinoschisis. In cases in which photocoagulations were performed, marked alterations were observed in postoperative SCE functions. Abnormal SCE functions have been noted in other types of retinal pathology as well (Fankhauser and Enoch, 1962; Dunnewold, 1964; Enoch et al., 1973; Pokorny et al., 1977; Smith et al., 1977; Campos et al., 1978; Fitzgerald et al., 1978). However, not all retinal disease, nor even all affecting the photoreceptor and pigment epithelial layers, disturbs retinal receptor alignment. For example, an essentially normal SCE function has been measured in a case of Best's disease (Benson et al., 1975) in which a large egg yolk-like lesion apparently lifts the retina from the pigment epithelium.

What is more instructive from cases of pathology is that following disturbance, a realignment of photoreceptors, as reflected in the recovery of the SCE function, may occur in tandem with the resolution of the pathological condition. The first indications that recovery was possible were seen in a case of retinal degeneration in which photocoagulation was performed (Fankhauser et al., 1961) and, more clearly, in a case of serous retinal detachment (Fankhauser and Enoch, 1962). Virtually complete recovery of SCE functions has been documented in cases of total retinal detachment (Enoch et al., 1973) and of subretinal fluid subsequent to trauma (Campos et al., 1978). In the latter case, there was evidence that receptor reorientation occurred within the macular region at the same time that the SCE function of a paramacular location, apparently outside the region of the primary lesion, showed deteriorative changes. Subsequently, this paramacular test location also showed the recovery of a normal SCE function. Marked improvement of a severely disturbed SCE function has recently been seen in a case of senile macular degeneration as well (Fitzgerald et al., 1978).

Dunnewold (1964) reported a patient with an iris coloboma, resulting in a displaced pupil, in which the SCE function peaked near the center of the displaced rather than physiologic pupil. Bonds and MacLeod (1978) have documented a similar case, in which a displaced pupil resulted from insult to the eye; both photopic and scotopic SCE curves were symmetrical about a point near the displaced pupil

center. It is possible that both of these instances also represent a "recovery" of receptor orientation to abnormal situations of retinal illumination.

It is significant that in eyes in which anomalous SCE functions have been demonstrated to accompany observable retinal pathology, other visual functions, including visual acuity, have also shown adverse changes (Fankhauser and Enoch, 1962; Enoch at el., 1973; Campos et al., 1978; Fitzgerald et al., 1978). In cases in which the SCE function has been found to recover, visual acuity has also shown improvement.*

Ohzu et al. (1972) and Ohzu and Enoch (1972) observed that the modulation transfer function, indicative of the optical resolution capability, of isolated retinas is markedly inferior in areas in which receptors are poorly oriented as compared with regions of well oriented receptors. Such observations have been made in rat retinas and in squirrel monkey and human foveas. Unfortunately, a characterization of the extent of malorientation of receptors in poorly oriented areas could not be specified quantitatively. This is a very complex problem.

Campbell (1958) reported psychophysical evidence for decreased resolution of grating targets entering the pupil at peripheral locations and presumably imaged obliquely onto

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* It is clear that visual acuity changes in these cases may also represent other aspects of the pathological process than the inferred changes in receptor orientation.

foveal photoreceptors. Resolution was poorer for targets oriented perpendicularly to the pupillary test meridian than for targets oriented parallel to it. Later work indicated that much of the effect could be attributed to aberrations suffered along peripheral optical paths in the eye (Campbell and Gregory, 1960; Green, 1967; Enoch, 1971). However, a small effect was found to persist even with interferometrically formed targets (Campbell and Gregory, 1960; but also Green, 1967). Enoch and Glismann (1966; Enoch, 1971) saw a reduced resolution capability in rat and monkey isolated retinas for changes in angle of the incident light. Both meridional and non-meridional effects seemed to contribute to the measured resolution decrement. The change in observed resolution for an 8° shift in angle of incidence was on the order of 10 to 20 per cent, much smaller than the resolution losses reported by Ohzu et al. (1972; Ohzu and Enoch, 1972) in areas of poor receptor orientation. However, the latter represented alterations in alignment in excess of 8°.

SCE anomalies have been demonstrated in some amblyopic eyes, from which gross pathology of the retina can be excluded [Enoch, 1957; 1959a, b; 1967a; Dunnewold, 1964; Marshall and Flom, 1970; Bedell, 1974 (reviewed in Chapter III)]. Photoreceptor malorientation, which may be inferred from SCE abnormalities, has been suggested to play a part in the decreased visual acuity of amblyopic eyes (Enoch, 1957; 1967a). However, the reduction in resolution which could be expected to result from photoreceptor orientation anomalies is modest in terms of that found in profound amblyopias.

It is uncertain whether the receptor orientation anomalies, which have sometimes been detected in amblyopes, represent a sign of microscopic pathology in the outer retina, a failure of the normal receptor alignment mechanism, or the sequelae of transient retinal pathology during infancy, which has otherwise resolved (Burian and von Noorden, 1974). To confound the situation even further, SCE functions which are significantly decentered with respect to the pupil are occasionally reported for presumably normal eyes (Flamant and Stiles, 1948; Westheimer, 1968; Wijngaard and van Kruysbergen, 1975). Based upon Enoch and Glismann's results, significant resolution losses would not be expected for a modest "simple tilt" of the receptors, i.e., the maintenance of good alignment between neighboring receptors but an overall orientation tendency toward a noncentral region of the entrance pupil. The histological evidence presented above, the results in retinal pathology, and microwave simulation studies (Enoch, 1960), all suggest that a general malorientation of the receptors, a loss of alignment between neighboring elements, would more significantly disturb resolution capacity.

The Transient Stiles-Crawford Effect and Directional Light Adaptation

Makous (1968) reported that if two fields, which had been equated for the SCE and which entered the eye at opposite sides of the pupil, were interchanged, this exchange

was marked by a sudden increase in brightness, followed by a slow decline to a lower steady state value. When these two fields were alternately employed as the surround upon which a small incremental test field appeared, a sudden rise in the increment field threshold, on the order of 0.7 log units, was found to occur when the surround beams were exchanged. Thereafter, the increment threshold returned to an asymptotic value with an apparently exponential course and a half time of 10 - 25 sec, depending upon the surround field luminance. Curiously, the recovery was slower for dimmer background fields. The increment threshold results seemed to mirror the subjective perception in all respects.*

Confirmation of this so-called transient SCE appeared in the work of Heath (1970), Bailey (1974), and Sansbury et al. (1974). Heath noted that fields compensated for the SCE and entering the pupil at disparate points demonstrated flicker when interchanged at a moderate rate. Bailey pursued this finding in his dissertation and was able to define directional sensitivity functions much narrower than the standard psychophysical SCE function, utilizing the criterion of critical flicker frequency. Sansbury et al. replicated Makous' original experiment using monochromatic, rather than white, test and surround fields and confirmed his report in all particulars. They also demonstrated, as had Makous,

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*Makous (1977) has recently reported that a transient reduction in visual resolution capability occurs under similar experimental conditions. He reports the magnitude of this reduction to be about a factor of two.

that both the magnitude and time course of the transient SCE were independent of the pupil entry position of the incremental test beam. Finally, they showed that in the steady state condition, the threshold raising properties of surround fields entering at opposite sides of the pupil were linearly additive. Both Makous and Sansbury et al. argued on the basis of their experiments that the transient SCE indicated the existence of receptors or channels with a directional sensitivity smaller than the aperture of the dilated pupil. However, they concluded that the effect was not the result of a preferential light adaptation of different groups of receptors by background beams incident at the retina at different angles. Coble and Rushton (1971) measured the fraction of cone pigment bleached in the fovea densitometrically, using a measuring beam which was varied in its pupil entry position, and also concluded that bleaching did not occur differentially in groups of cones with dissimilar orientations. While MacLeod (1974) also failed to find psychophysical evidence of directionally selective light adaptation at the fovea, he did elicit such an effect at 6° in the parafovea. In contrast to the foveal results, he found that the entire SCE function shifted slightly depending upon the entry position of a background beam in the pupil; for peripheral pupil entry positions, the difference between the curves was approximately 0.3 log units.

Both the transient SCE and the apparent entoptic visualization of receptor subgroups (see above) seem to indicate

the existence of at least modest variation in receptor orientation. This implies that the directional sensitivities of individual receptors might well be narrower than the SCE curve, also indicated by microspectrophotometric analyses of single receptors in vitro (see Enoch, 1975). However, there is as yet no adequate explanation for the transient SCE. Makous noted that the transient SCE was similar in time course, magnitude and the effects of varying luminance to a phenomenon described by Baker (1949) in conjunction with rapid light adaptation. It would seem that contrary to Makous' argument that the two phenomena are unrelated, sufficient similarity exists to actively pursue a connection. In particular, both effects may reflect processes initiated by a transient signal from (groups of) photoreceptors but which occur at a more proximal site.

Stiles-Crawford-like Effects in Infrahuman Species

There have been relatively few attempts to identify Stiles-Crawford-like effects in animal models. The existing data are in the form of retinal electrophysiological responses to different angles of incidence of a test illumination.

Donner and Rushton (1959) recorded ganglion cell responses to a flashed incremental field presented against a steady adapting background from a frog eyecup preparation. Ganglion cell threshold was found as the angle of incidence of the incremental beam at the retina was varied. The authors were careful to direct the test field image onto a portion

of the ganglion cell receptive field remote from the recording electrode, in order to avoid potential shadowing artifacts. The test illumination, necessary to produce a criterion ganglion cell response, changed 0.4 - 0.8 log units over a 15° range of angles of incidence when the preparation was photopically adapted. Scotopically, changes in the angle of test beam incidence had no measurable effect upon ganglion cell threshold.

Tobey et al. (1975) report similar unpublished experiments by Reynauld and Laviolette, in which a directional sensitivity was found under photopic conditions for goldfish retina, as assessed by ganglion cell responses.

Baylor and Fettiplace (1975), using the turtle eyecup, recorded slow potentials intracellularly from photoreceptors while changing the angle of the incident light. The authors report clear sensitivity changes in "red" and "green" cones as a function of the angle of incidence and possibly smaller effects in "blue" cones and rods, which were encountered less frequently. Pautler (1967) had earlier found evidence for directional sensitivity of turtle receptors in an isolated retina preparation. He noted changes in the magnitude of the S-potential when the angle of incident light was varied.

Stiles-Crawford-like effects in this preparation are modified by the presence of high refractive index, absorbing oil droplets between cone inner and center segments. These have differential absorption of incident light depending upon its angle, due to changes in path length through the oil

droplets. However, the oil droplet absorption should tend to reduce rather than enhance measured Stiles-Crawford-like effects in turtle cones. Baylor and Fettiplace report that the magnitude of the directional sensitivity effect, for a given cell, depends upon the wavelength of the incident light, directional sensitivity becoming less or "inverting" (i.e., a greater sensitivity to presumed off-axis light) for wavelengths away from the cell's sensitivity maximum. These curious wavelength effects may be largely or wholly attributable to the directionality of the oil droplets, that is, their lesser absorption of obliquely incident light.

Baylor and Fettiplace conclude that the directional sensitivity of individual turtle receptors is fairly broad, corresponding well with the angular subtense of the turtle eye pupil at the retina. This conclusion is in contrast to optically determined directionalities of single photoreceptors in other species. Enoch and coworkers have determined the angular radiation patterns of single goldfish, frog, and rat photoreceptors when retroilluminated in isolated retina preparations (e.g., Tobey et al., 1975). On the basis of Helmholtz's theorem of optical reciprocity, i.e., the equivalence of forward and backward passage of radiant energy through an optical system, Enoch has argued that the angular radiation pattern specifies the angular acceptance pattern, or the optical directional sensitivity. Directional sensitivities of single receptors, derived in this way, are considerably narrower than either the angular subtense of the pupil or of

the optical directional sensitivities of large groups of receptors. Differences between rods and cones are quantitative rather than qualitative. Enoch (1961a; 1967b) has also made similar observations when light is passed through receptors in the physiologic direction, i.e., from inner retina to outer retina. That is, varying the angle of incidence of a light beam on the retina by only a few degrees greatly alters the transmissivity of individual rods and cones as observed in numerous mammalian species, including humans. It should be stressed that these optical measurements and observations have been made in species without receptor oil droplets.

Electrophysiological determinations of Stiles-Crawford-like effects in animals are potentially a very powerful tool for understanding basic receptor directional sensitivity processes. Thus, electrophysiologically determined directional sensitivities of single receptors and of ganglion cells in the same preparation might indicate the role of variations of individual receptor alignment in the psychophysical SCE. The use of preparations with noncircular pupils, measuring directional sensitivities for two or more pupillary axes, could suggest mechanisms involved in maintaining receptor alignment. The difficulties involved in such studies are also tremendous, however. In an eyecup or isolated retina preparation, specification of receptor alignment relative to the eye's pupil is difficult. The effects of the electrode itself upon the stimulating light are uncertain. This is

an especially difficult problem when intrareceptor recordings are attempted since the mere presence of the recording electrode in proximity to the photoreceptor must perturb light propagation along the receptor. Obviously, electrode penetration can also influence cellular orientation. It is not clear what kind of controls are possible to avoid potential artifacts from such sources. However, the direct observation of the optical properties of the receptors studied is indicated.

Theory

The first important theoretical issue concerning the SCE was whether it is primarily retinal in origin or an effect of preretinal absorption. Stiles and Crawford's (1933) own calculations indicated that estimated preretinal absorption (and reflection) differences between beams passing through the center and periphery of the pupil were small compared to the magnitude of the psychophysically measured effect. Experiments by Craik (1940) and Goldmann (1942) further indicated that the phenomenon was probably retinal in origin. Weale's (1961) analysis of the effect of lens absorption indicated that this, in fact, reduced the magnitude of the psychophysical SCE. Differences between normal photopic and scotopic SCE functions (Crawford, 1937; VanLoo and Enoch, 1975) and changes seen over time in the SCE of observers with retinal pathology (Fankhauser et al., 1961; Fankhauser and Enoch, 1962; Enoch et al., 1973; Campos et al., 1978; Fitzgerald et al., 1978) also indicate a retinal basis.

Wright and Nelson (1936) proposed, virtually in passing, that the directional sensitivity of the retina might derive from the light trapping properties of retinal receptors. That is, light incident upon receptors normally to their long axis, or at very shallow angles to the normal, might be expected to suffer total internal reflection and hence remain within the receptor for its entire length. On the other hand, light incident at more oblique angles to the normal would no longer be contained by internal reflection but rather be refracted out of the receptor into the intercellular space. Rays leaving the receptor would, of course, have a lower probability of encountering, and therefore exciting, visual pigment rendering these rays visually less efficacious. The same concept had been proposed by Brücke (cited in Helmholtz, 1924) some 90 years earlier.

O'Brien (1946, 1951) further developed the concept of total internal reflection within receptors as a possible basis for the SCE, stressing the importance of the ellipsoid, coupling the inner and outer segments, and its taper angle. Within his framework, light losses from receptors occurred primarily within or near the ellipsoid region. O'Brien's model brought attention to the possibility that photoreceptors might concentrate light from the larger diameter inner segments into the narrower outer segments. In fact, light collection has been directly observed in retinal photoreceptors (Tansley and Johnson, 1956; Enoch, 1961a). Psychophysical evidence, which suggests that human receptors concentrate

light, has been provided by Brindley and Rushton (1959) and Brindley (1959).

Toraldo di Francia (1949) pointed out that the dimensions of retinal receptors are on the order of the wavelengths of visible light; hence, receptor optical characteristics could not be adequately specified by the geometrical optical approaches such as Wright and Nelson and O'Brien had proposed. Toraldo drew an analogy between photoreceptors and dielectric antennae, suggesting not only the application of physical wave optics but also the usefulness of the optical reciprocity theorem, i.e., that angular radiation and acceptance patterns of receptors are identical.

Further analyses of the SCE have generally begun with the presumption that receptors act as optical waveguides. Waveguide properties are ascribed on the basis of the dimensions of receptors, which in cross section are on the order of wavelengths of light, and on the higher refractive indices measured for receptors than for surrounding extracellular material (Barer, 1957; Sidman, 1957; Enoch and Tobey, 1978).

Energy passes along waveguide structures in characteristic interference patterns or modes, which depend upon the receptor geometry (morphology), size and refractive index relative to the surrounding material as well as upon the wavelength and angle of incidence of the exciting light (Enoch, 1961a, b, c; Enoch and Horowitz, 1974). Such modal patterns have been observed in the receptors of many vertebrate species (Hannover, 1843, cited in Enoch and Tobey, 1973; Enoch,

1961a, b, c; MacNichol, 1967; Enoch and Tobey, 1973; Tobey et al., 1975). Moreover, observed modal patterns may be altered by a change of wavelength or of the angle of incidence of the exciting light (Enoch, 1961a, b, c; Enoch and Tobey, 1978). The modal patterns seen are those which would be predicted on the basis of photoreceptor dimensions and indices of refraction.

Waveguides evidence directionality in the sense that energy incident at some angles is accepted preferentially over that at others. As noted above, optical studies of vertebrate receptors indicate a high degree of directionality, both in rods and in cones. Lesser directionality is found for groups of receptors than for single elements (Enoch, 1975). Waveguides also tend to concentrate light, in that their effective light capturing area is typically larger than their geometrical cross sectional dimension (Snyder and Hammer, 1972). Psychophysically determined retinal directionality is thus seen to be in good qualitative agreement with the optical waveguiding properties of retinal receptors based upon their physical structure.

Snyder and Pask (1973, also Pask and Snyder, 1975) and Wijngaard and van Kruysbergen (1975, also Wijngaard et al., 1974) have proposed models of the SCE based on physical wave optical treatments. In such analyses, receptor dimensions, refractive indices of the receptors, of their subregions, and of the extracellular interstitial matrix and associated structures are important parameters. These models

require specification of the physical parameters noted above with high accuracy as well as simplifying assumptions as to receptor geometry and homogeneity. Unfortunately, the physical measurements made to date of photoreceptors and their natural retinal milieu fail to reach the accuracy demanded, essentially because of limitations inherent in available measurement techniques (but see Barer, 1957; Sidman, 1957; Enoch and Tobey, 1978). This makes an evaluation of such models difficult, since all of them can be made to reasonably fit the psychophysical data by suitable adjustment of parameters.

An important issue for all models of the SCE is the extent to which the psychophysical function represents the directionality of single receptors, rather than an averaged directional tendency of a population of small acceptance angle receptors with interreceptor scatter in orientation (Crawford, 1937; Safir and Hyams, 1969; Safir et al., 1971). Present evidence seems to favor the latter view, since (1) optical specification of acceptance angles of individual receptors of several species indicates small (2° - 4°) half angles (Enoch, 1975); (2) apparent local variations in receptor pointing can be demonstrated entoptically (O'Brien, 1950; Enoch, 1967a; Heath and Walraven, 1970; Enoch et al., 1978); (3) the transient SCE and directional light adaptation demand at least a modest nonuniform directional sensitivity at some level in the visual system [although the nonuniformity might lie <u>within</u> individual receptors (see King-Smith, 1974;

Sansbury et al., 1974; Crawford, 1972)]; (4) Bailey (1974) has measured narrow directionality SCE functions using a critical flicker fusion technique. On the other hand, fundus reflectometry indicates no measurable receptor scatter at the fovea in terms of bleaching (Coble and Rushton, 1971) and the single electrophysiological study of the directional sensitivity of single retinal receptors (which is subject to the limitations described above) finds broad acceptance angles which fill the pupil (Baylor and Fettiplace, 1975).

Laties and Enoch (1971) have demonstrated that retinal histology can be of little help in assessing the small angular differences in neighboring receptor orientation which may be involved. Further intrareceptor electrophysiology and optical studies of single receptors and groups of receptors are important. Psychophysically, an understanding of the transient SCE might aid in the resolution of this question. A note of caution: It is not unreasonable to assume that, in different species or at different retinal locations within the same species, contributions of the acceptance angles of individual receptors, of interreceptor orientational scatter and of neural summing across groups of receptors to the SCE might differ in importance.

The Stiles-Crawford Effect of the Second Kind (SCE II)

Basic Experimental Data

When the SCE is measured for monochromatic lights, using a direct photometric matching technique, a comparison field

which enters the pupil displaced from the center may undergo not only a change in brightness but in perceived hue as well. This hue shift has come to be known as the Stiles-Crawford effect of the second kind (SCE II).

The first detailed description of the SCE II was by Stiles (1937). He presented observers with a bipartite field which was to be matched for both hue and brightness.* Standard and comparison half fields derived from two monochromators, the exit slit of the first imaged at the center of the observer's pupil. The comparison field beam, from the second monochromator, was imaged successively at half mm intervals across the width of the dilated pupil. The observer controlled both the luminance and wavelength of the comparison beam, thereby permitting him to match the standard half field, which was set at one of 11 wavelengths spanning the visible spectrum.

The SCE II functions reported by Stiles (change in apparent wavelength vs. pupil entry position of the comparison beam) are complex in shape. Despite a general resemblance

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*In measuring the SCE II, a brightness match between comparison and standard half fields, in order to compensate for the SCE (of the first kind) is required in order to avoid contamination of the SCE II by the Bezold-Brücke hue effect. The latter is the change in apparent hue which occurs with changes in luminance. In general, as luminance is decreased, hues shift toward a greener or redder appearance (see, e.g., Boynton and Gordon, 1965). The magnitude of the Bezold-Brücke effect, for a 1.0 log unit change in luminance, is comparable to that of the SCE II. The two effects are dissimilar in many particulars, the respective hue shifts being in opposite directions in many regions of the spectrum.

to SCE curves, several of the functions seem not to be symmetrical about the peak of the simple SCE function. Since all lights were essentially monochromatic, lens or other preretinal absorptions cannot be responsible for these asymmetries.

With a few exceptions in midspectrum, most of the hue shifts are toward longer apparent wavelengths. This is in contrast to the Bezold-Brücke hue shifts which are toward both shorter or longer wavelenghts in various regions of the spectrum.

Walraven and Bouman (1960) presented SCE II hue shift data for comparison beams entering the pupil 3.5 mm from the SCE peak. Wijngaard and van Kruysbergen (1975) also present SCE II data for a single observer. Neither study gives any particulars whatsoever as to measurement techniques; however, the results agree qualitatively with both Stiles (1937) and later work by Enoch and Stiles (1961).

Stiles (1937) noted that for most wavelengths, comparison and standard fields differed not only in (brightness and) hue but in saturation as well. In the blue-green region of the spectrum, a beam passing through the periphery of the pupil appeared more saturated than one entering at the center. Enoch and Stiles (1961) thus addressed the problem of specifying a complete color match (hue, lightness, and saturation) between fields entering at the center and periphery of the pupil. Standard and comparison monochromatic beams, of the same wavelength, were brought to match by the

addition of small amounts of fixed primary lights to one or both fields, i.e., by trichromatic colorimetry. Standard fields were adjusted in luminance to an equal luminance spectrum. Enoch and Stiles' results, specifying the complete SCE II color change, are given in terms of Wright's u, v, w color coordinate system. From these data, the apparent shift of the spectrum locus for the principle observer for a beam 3.5 mm from the simple SCE peak could be specified. The calculated shifts of dominant wavelengths coincide well in a qualitative way with SCE II hue shifts reported for other observers. Note that the SCE II color shift is specified in stimulus terms; an indication of the perceptual color shift as a function of wavelength might be gotten by a transformation of observer JME's data (Enoch and Stiles, 1961) from Wright's u, v, w color space to one of the more nearly uniform chromaticity spaces (Wyszecki and Stiles, 1967).

Brindley (1953) investigated the effects of intense adapting lights on color matching. In one of his experiments, he matched a monochromatic yellow with a mixture of red and green lights, all beams entering at the center of the pupil. When the pupil entry position of all stimuli was shifted to 3 mm from center, the match no longer held. (Unfortunately, the spectral characteristics of Brindley's matching lights were shaped by relatively broad band filters and hence, differential lens absorption as a function of wavelength for the two pupil entry positions may have played some role in his results.) This phenomenon was, of course, much more

extensively studied in the later Enoch and Stiles work. However, Brindley further observed that after adaptation to an intense (10^4 td) yellow field, an SCE II hue shift was no longer seen for a monochromatic yellow light, when its entry position was shifted in the pupil. The observer could still discriminate actual wavelength changes of the stimulus after the intense light adaptation, however. Brindley's results indicate that, at least for a single wavelength, the SCE II hue shift could largely be nullified by intense light adaptation.

Wooten et al. (1977) reported in a preliminary communication that an SCE effect does persist at high bleaching levels. The high intensity SCE II apparently differs both qualitatively and quantitatively from that reported for lesser retinal illuminances.

The Stiles-Crawford Effect of the Second Kind in Anomalous Vision

Walraven and Leebeck (1962) measured the SCE II hue shift in single deuteranomalous and protanomalous observers. The hue shifts of both observers were larger than those obtained in color-normals; this only emphasizes the necessity of expressing SCE II hue shifts in perceptual rather than stimulus terms, i.e., the color anomalous' hue discrimination functions were presumably not as acute as those of color normals (Wright, 1946). The color anomalous observers reported increased saturation as well as hue changes for some wavelengths entering peripherally in the pupil. The most curious

aspect of the data is that for wavelengths greater than 500 nm the hue shifts were pronouncedly toward shorter wavelengths for both anomalous observers, in contrast to the shift toward the red described by color normals above ca. 560 nm.

Since receptor malorientation has been described in certain visual pathologies, including some amblyopic observers (see above), Alpern et al. (1967) looked for a change in anomaloscope matches in strabismic amblyopic eyes as an indicator of retinal receptor tilt. (Earlier observations of anomalous SCE functions in some amblyopic eyes had been made on nonstrabismic amblyopic subjects having limited acuity decrements.) The rationale was that if cones in his sample of amblyopic eyes were tilted, one might expect a slight hue shift toward the red in the amblyopic eyes' anomaloscope matches, corresponding to the SCE II hue shift for yellow light. No clear evidence of a hue shift was found; however, a number of technical objections to the experimental procedure can be made. On the other hand, Pokorny et al. (1977) not only found disturbed simple SCE curves in several cases of senile macular degeneration, but also noted abnormal anomaloscope matches for various matching field sizes in the same eyes. The authors have suggested that these results may be understood in terms of an SCE II-like hue shift toward longer wavelengths as the result of maloriented receptors in their subjects. This interesting hypothesis would seem to require additional verification, such as determinations of SCE II functions in these anomalous eyes.

Stiles-Crawford Effect of the Second Kind: Theory

Very early on, Stiles (1937) entertained the idea that SCE II changes resulted from different directional sensitivities of the fundamental cone mechanisms. Although this must certainly play some role in the SCE II, Stiles' calculations indicated that another factor or factors must also contribute to the color changes.

One possibility is contained in the so-called self-screening hypothesis. Briefly, this is based on the observation that pigment absorption characteristics change with the effective density of the pigment in its substrate medium, or alternatively, with the path length through a solution of given pigment concentration (e.g., Walraven and Bouman, 1960). Stiles, and later Brindley (1953), Walraven and Bouman (1960), and Enoch and Stiles (1961) noted that light entering the pupil away from the center would strike well-oriented receptors at an oblique angle and hence, rather than pass down the whole absorbing length of the outer segment might "leak" out after traversing only some fraction of this distance. Hence, for nonsmall pigment densities, the spectral absorption of such receptors would depend upon the angle at which incident light strikes the receptors.

Enoch (1961a, b; 1963) reported that the outer segments of bleached photoreceptors illuminated with white light appeared as a multicolored mosaic of modal patterns. Changes of the angle of the incident light not only altered the modal patterns but also the distribution of hues observed (Enoch, 1961a, 1963). In general, increased obliquity of incident

light resulted in an increased transmission of long and short wavelengths and lesser transmission of middle wavelengths in bleached receptors. Enoch's observations indicate that receptor waveguiding properties must be taken into account not only in the SCE brightness phenomenon but in SCE II color effects as well.

Walraven and Bouman (1960) proposed a theory of both the SCE II and the wavelength dependence of the SCE of the first kind based upon the self-screening hypothesis and geometrical optical considerations. Later Wijngaard et al. (1974) revised this model in light of the physical optical characteristics of retinal receptors. Enoch and Stiles (1961) showed that self-screening did not adequately account for all aspects of their data, assuming geometrical optics and light "leakage" from receptors independent of wavelength. It is not clear that physical optical considerations, as applied by Wijngaard et al., provide a superior fit to the data. While such models appear to be on the right track, current knowledge of the physical constants involved is insufficient to permit meaningful evaluation of such modelling attempts.

Significance of the Stiles-Crawford Effect

The SCE or Stiles-Crawford-like effects have been demonstrated in frog (Donner and Rushton, 1959), goldfish (Reynauld and Laviolette, cited in Tobey et al., 1975), turtle (Pautler, 1967; Baylor and Fettiplace, 1975) and humans. Optical studies of isolated retinas of goldfish, frog, rat,

and humans have indicated directional sensitivity of individual receptors or of small groups of receptors in these species (Enoch, 1975). Directionality has shown for both rod and cones. It thus seems that directional sensitivity may be ubiquitous in vertebrate photoreceptors.

Laties and coworkers found that photoreceptors at all positions of the retina tended to align to a common region at the anterior part of the eye, presumably near the center of the exit pupil. Such anterior pointing of photoreceptors has been seen in fish, amphibian, reptile, bird, mammal, and primate retinas (Laties et al., 1968; Laties, 1969; Laties and Enoch, 1971; Enoch, 1972; Enoch and Horowitz, 1974; Baylor and Fettiplace, 1975). The peak of the SCE function of human observers has been shown to remain near the center of the exit pupil of the eye for test locations up to 20° in the nasal visual field and 35° in the temporal visual field (Enoch and Hope, 1972a, Enoch and Hope, 1973; Bedell and Enoch, 1978). The psychophysically determined SCE thus apparently reflects the retinal photoreceptor orientation and complements the histological findings. Additionally, in some species with reflecting tapeta, the tapetal reflecting surfaces have been demonstrated to be oriented approximately perpendicularly to a hypothetical ray passing through the center of the exit pupil (Denton and Nicol, 1964; Nicol, 1969; Enoch, 1972).

The rather precise alignment of retinal structures with what is apparently the exit pupil of the eyes of diverse species raises two obvious questions. The first is teleological: What is the purpose of such alignment? The

second question is how this alignment is established and maintained. Answers to both must be somewhat speculative.

The SCE has often been suggested to serve a contrast enhancing function (e.g., Beck, 1950; Enoch, 1972). Whereas the eye pupil is the source of relevant visual signals, such signals may be degraded by the presence of contrast reducing scattered light within the eye. Directionally sensitive receptors which are aligned toward the region of the exit pupil of the eye are presumably maximally sensitive to light entering through the pupil and less sensitive to more obliquely incident light scattered from within the retinal sphere. In this regard, it has been noted that human photopic and scotopic SCE contours correspond to the relatively constricted and dilated pupils typical of the respective adaptive conditions (e.g., Stiles, 1962). Thus, rods are relatively more sensitive than cones to light entering near the edge of the dilated pupil, a region which can only be a source of stray light under photopic adaptation. In species in which the pupil performs an apodizing function, by virtue of an asymmetric or exotic shape, a correspondence between Stiles-Crawford-like contours and the pupillary aperture is more questionable, albeit experimentally testable.

A tendency for photoreceptors at all regions of the retina to align toward the center of the exit pupil permits the optimal utilization of the receptors' directional sensitivity properties across the entire retina. Were the receptors perpendicular to the pigment epithelial substrate

throughout the eye and yet directionally sensitive, at retinal locations remote from the posterior pole, sensitivity to stray light would be enhanced at the expense of sensitivity to visual signals entering through the pupil. Moreover, photoreceptor alignment toward the exit pupil of the eye presents the greatest density and path length of photosensitive molecules, aligned in transverse stacks of outer segment discs, to light entering the eye pupil.

In terms of reducing sensitivity to intraocular stray light, the effect of the lens upon the SCE may also be considered. Lens pigments tend to reduce the magnitude of the SCE measured psychophysically with respect to the presumed underlying directional sensitivity at the retina. Thus, the retinal sensitivity to intraocular stray light is actually less than that indicated by the magnitude of the psychophysical SCE. The greater magnitude of the SCE in the blue and red regions of the spectrum may be understood in terms of a further reduction of sensitivity to the stray light within the eye. Intraocular scattered light is presumably greater at short wavelengths, due to Rayleigh scattering, and at long wavelengths, as the result of reflections from vascular tissues, than at middle wavelengths.

As recognized by Brücke (cited in Helmholtz, 1924), the orientation of tapetal surfaces perpendicularly to rays entering the center of the exit pupil of the eye tends to pass reflected light from the tapetum through the same photoreceptors that were traversed during the forward passage through

the retina, potentially aiding resolution. Additionally, light which is not absorbed within the receptors after tapetal reflection has been redirected toward the pupil, and hence tends to leave the eye rather than increase stray light levels within the eye.

An obvious consequence of the SCE is that the effective stimulus for visual response cannot be simply specified in terms of retinal illuminance. The distinction between distal and proximal stimuli (Riggs, 1965) becomes rather complicated. LeGrand (1968) has proposed the effective troland as a unit of retinal illuminance, in which compensation for the SCE has been incorporated. Some of the pitfalls inherent in defining and applying a standard SCE function integrated across the pupil were considered above. Additionally, markedly different SCE corrections are necessary for photopic and scotopic vision and the change from scotopic to photopic values occurs over a considerable range of mesopic illuminances, ca. 1-1/2 to 2 log units (Crawford, 1937; Stiles, 1939). It is not immediately apparent how SCE corrections might be incorporated into photometry in a standardized, and as yet meaningful, way.

Vos (1960, 1966) has pointed out that an SCE peak which is decentered in the pupil tends to shift the effective pupil center, i.e., the location of the center of gravity of all the light entering the pupil when individual rays have been weighted for their luminous efficiencies, from the geometric pupil center toward the location of the SCE peak. In fact, perfect centration of the SCE is not often found in normal

observers. Vos has argued that individual differences in the magnitude and the direction of chromostereoscopic effects may be explained when the disparity between the effective and geometrical pupillary centers is considered. He has presented SCE data for several observers which tend, at least qualitatively, to support these conclusions.

Since visual resolution is more dependent upon the presence of optical aberrations than upon the small changes in target brightness which might occur on either side of the SCE peak, maximal resolution is found for light entering at the pupil center (Campbell and Gregory, 1960; Enoch, 1971). Thus, to a limited extent, the effective pupil centers for brightness and for resolution may differ in position. In one case of a displaced pupil, the best visual acuity was achieved for target beam entry 2-1/2 mm from the SCE peak (Bonds and MacLeod, 1978). Clearly, such a disparity may be of importance in the use of subjective alignment to artificial pupils or to a Maxwellian view system.

The mechanism or mechanisms by which photoreceptor (and tapetal) orientation are established and apparently maintained are unknown. Precise photoreceptor orientation has been histologically demonstrated to exist prior to birth in chick and monkey eyes (Laties and Enoch, 1971; Enoch, 1972). In the latter instance, the eye was not exposed to light prior to histological processing of the retina. Demonstrations that the SCE can recover after disturbance (Fankhauser and Enoch, 1962; Enoch et al., 1973; Campos et al., 1978; Fitzgerald

et al., 1978) and that it apparently "recovers" toward the center of displaced pupils (Dunnewold, 1964; Bonds and MacLeod, 1978) suggest the operation of a postnatal mechanism which maintains receptor alignment. The recovery of human receptor orientation subsequent to pathological disturbance has been demonstrated to occur in as short a period as three weeks (Campos et al., 1978). In this regard, the continuous renewal of photoreceptor outer segments, with a time course of 9 - 12 days in rhesus monkey rods (Young, 1976), is provocative. However, Enoch (1972) has noted that receptor orientation at retinal locations away from the posterior pole seems to result from a relative bending of the inner segments at the external limiting membrane rather than at the connecting cilium joining the inner and outer segments.

It is seen that the orientation of photoreceptors and associated structures with respect to the source of relevant visual stimuli is apparently a common characteristic of vertebrate, and also of a large number of invertebrate (Snyder and Menzel, 1975) visual organs. On the basis of their physical properties, the photoreceptors of these diverse species apparently uniformly exhibit a directional sensitivity to incident light as well. The SCE is a sensitive psychophysical function which, according to current evidence as presented here, reflects the underlying directionality and orientation of retinal photoreceptors.

Teleologically speaking, the prevalence of photoreceptor orientation and directionality across numerous species

indicates a highly significant role for these specializations in the visual process. At this time, neither the mechanisms which establish and maintain directionality and orientation nor their complete role in vision are well worked out. Because the orientation and directionality of photoreceptors must intimately bear upon the primary phases of the neural visual response, these factors and their significance must be understood in order to meaningfully evaluate their influence upon subsequent visual processing, both in normal and in pathological conditions.

CHAPTER III
A BRIEF REVIEW OF FUNCTIONAL AMBLYOPIA AND OF STILES-CRAWFORD FUNCTION MEASUREMENTS IN AMBLYOPIC EYES

The nature of the anatomical and physiological changes which occur in functional amblyopia are as yet unknown. The search for such changes is hampered by the high probability that amblyopia is not a unitary syndrome with a single underlying pathophysiology. On the contrary, anomalies at any number of sites within the visual system might give rise to a decreased acuity.*

In the current literature, interest focuses on the dorsal portion of the lateral geniculate nucleus (LGN) and even more so, on the primary visual cortices. Wiesel and Hubel (1963a, b) demonstrated morphological changes in dorsal LGN neurons and alterations of ocular driving patterns of visual cortical neurons in monolaterally sutured kittens. More recently, functional neuronal connections have been shown to be altered in monkey striate cortex following unilateral eyelid suture or experimentally induced strabismus or anisometropia (Hubel and Wiesel, 1977; Baker et al., 1974; von Noorden and Crawford, 1977).

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*See footnote, Chapter I.

Suppression of the amblyopic eye during nonmonocular ("binocular") viewing is a common clinical and psychophysical finding in apparent accord with the cortical neurophysiological data. However, there are indications that changes may occur more distally in the amblyopic visual system as well. For example, amblyopic eyes are reported to evidence an excessive areal summation (or diminished inhibition), a function generally ascribed primarily to the outer retina (Flynn, 1967; Danis and Meur, 1967; Lawill et al., 1973). Ikeda and Wright (1974, 1976) measured electrophysiological contrast sensitivity functions for single neurons in the kitten LGN; responses presumably indicated contrast sensitivities of retinal ganglion cells. Neurons driven from the deviated eye of experimentally esotropic kittens showed losses of contrast sensitivity, especially sustained units (X cells) with receptive fields in or near the area centralis. These data not only implicate the retina as at least one of the sites of anomaly in this animal model of strabismic amblyopia, but also conform to the typical clinical and experimental finding of a deficit primarily localized to central vision in amblyopic eyes. That is, monocularly measured functions, including visual acuity, typically indicate the greatest disturbance at the center of the amblyopic eye visual field and approach (or attain) normal levels of functioning in the near periphery (Meur and Conreur, 1968; Kandel and Bedell, 1973; Kirschen, 1977).

It is the author's working hypothesis that functional changes in amblyopia may occur at virtually any level of the visual system. Because amblyopia is probably not unitary in its pathophysiology, discrete subgroupings may be identifiable, based upon the site or sites of the primary lesion or the evolution of the pathological process during development.* Since workers have seemed reluctant to recognize the possibility of functional subgroupings of amblyopia (but see Burian and von Noorden, 1974), there is little indication in the present literature as to what sort of divisions may be useful. Currently, functional amblyopias are distinguished on the basis of their inferred etiology, e.g., strabismic, anisometropic, deprivation, etc.

Information processing in the human visual system is primarily centrifugal, at least in its early stages. It is apparent that psychophysically or neurophysiologically demonstrated abnormalities, which are sampled at proximal sites within human amblyopic or experimentally induced amblyopic visual systems, might reflect either anomalies at that level of processing, or anomalous input from more distal sites, or both. It therefore seems reasonable to approach the pathophysiology of amblyopia in a disto-proximal direction,

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*For example, Sherman and coworkers (Sherman et al., 1972; Norton et al., 1977) reported selective loss of transient (Y) cells and apparent integrity of the X cell system in an animal model of form deprivation amblyopia. These results are in contrast to those of Ikeda and Wright, who used an animal model of strabismic amblyopia (see above).

i.e., to ascertain the status of the information passed along to subsequent stations from each "processing" center in the amblyopic visual system.

Advances have already been made in this line of attack. In post hoc analyses of a limited number of cases, the optical transfer properties (imaging capability) of amblyopic eye media were found not to be impaired relative to normal eyes (Fankhauser and Röhler, 1967; also Burian, 1967a). It is clear that this statement must be qualified in cases of amblyopia with anisometropia.

On the other hand, SCE function measurements have indicated the existence of anomalies in some amblyopic eyes at the next stage of the visual system, namely at the level of the photoreceptors. Based upon the evidence presented in the previous chapter, it is probably reasonable to suggest that psychophysically determined SCE functions represent (1) the directionality of individual receptors and their related structures, (2) some distributive orientation factor between receptors and between groups of receptors, and (3) possible neural integrative processes by which the outputs of groups of receptors are combined. Additionally, one may posit perceptual, criterion and/or judgmental factors, inherent in the nature of psychophysical measurements, which might derive from possible differences in the appearance of stimuli entering the pupil at different locations. It is likely that the contribution of some or all of these factors, as well as their relative importance, changes with position

on the retina and perhaps with other observer or stimulus variables as well. Such changes, should they occur, presumably modify the shape of and/or the directionality represented in psychophysically determined SCE functions. However, the location of the peak of the SCE function would seem to be a valid indicator of the overall alignment tendency of a group of retinal photoreceptors with respect to the pupil. SCE functions which show no clear peak, or multiple subpeaks, are assumed to indicate a "general malorientation" of the photoreceptors with respect to one another, i.e., the disruption or lack of a well-defined alignment tendency within the group of receptors sampled.

The SCE function has been found to be disturbed in some, but not all, amblyopic eyes. Enoch (1957, 1959a, b) found clearly anomalous SCE functions at the locus of fixation in two of six amblyopic observers tested. In these two observers, amblyopic eye SCE functions demonstrated marked departures from the typical paraboloid shape, appearing instead rather flattened and asymmetrical. Similarly disturbed SCE functions have been seen in cases of active retinal pathology, in which visual acuities have also been found to be reduced. It is clear, however, that the reduced visual acuities in these cases of retinal pathology might derive from factors in addition to inferred receptor malorientation. Moreover, the anomalous SCE functions determined for these amblyopic eyes and those determined in cases of observable retinal pathology cannot be assumed to have a common etiology. In

three other observers of Enoch's sample, amblyopic eye SCE functions had maxima, estimated from the positions of the peaks of horizontal and vertical pupillary traverses, displaced from the pupil center by between 1-1/2 and 2-1/4 mm. The nonamblyopic eyes of these observers all demonstrated normal appearing SCE functions, with peaks within 1 mm of the pupil center. For one amblyopic observer, normal appearing SCE functions were measured in both eyes.

Dunnewold (1964) measured SCE contours at the point of fixation in both eyes of each of two mildly amblyopic observers. He employed a clinical testing instrument (Vos and Huigen, 1962) without a biteplate and using a subjective alignment procedure. These factors, as well as his failure to show raw data or indicate error variance, render his results somewhat suspect. In one of his cases, the SCE function peak was displaced approximately 3 mm from the pupil center; however, the maximum of the SCE function of the nonamblyopic eye was itself 2 mm displaced. Other than decentration of the peaks, the functions of both eyes appeared normal. Dunnewold's second case was found to have normal SCE functions and centered peaks in both eyes.

Marshall and Flom (1970) measured SCE functions, in the horizontal meridian only, in four moderate and severe amblyopes. In two of these observers, both of whom fixated extrafoveally under monocular viewing conditions, SCE function peaks, determined at the locus of fixation, were subsubstantially displaced from the pupil centers. The SCE

functions of the nonamblyopic eyes all had peaks near the pupil centers and were normal in appearance. One of the eccentric fixators subsequently recovered a centric fixation in the amblyopic eye. At that time, a more centered SCE function was measured in this eye. Marshall and Flom, apparently assuming that photoreceptors align toward the center of the globe, rather than toward the exit pupil of the eye, argued that decentered SCE functions were to be expected in cases of eccentric fixation and might be an indicator of such noncentric fixation rather than of tilted foveal photoreceptors. As reviewed in Chapter II, recent psychophysical studies of normal eyes indicate that receptors at both central and peripheral retinal locations tend to align toward the eye pupil, contrary to the assumption of Marshall and Flom.

Bedell (1974) determined SCE functions in a single severe strabismic amblyopic observer, with a large eccentric fixation, at the locus of fixation and at several points nearby. All curves showed slightly displaced peaks and a lack of symmetry about the maximum value. Steadiness of fixation, which is of considerable concern when measuring SCE functions for strabismic amblyopic observers, was evident from the small variability of SCE function measurements and from the consistency of the data obtained over several months. SCE functions in the nonamblyopic eye were nearly centered.

Alpern et al. (1967) attempted to detect anomalies of the SCE functions of three strabismic amblyopic observers utilizing the SCE II effect (see Chapter II). Negative results were reported for all three observers. However, details of the testing procedure and certain questionable assumptions which the authors made regarding the SCE II make interpretation of this ingenious experiment difficult.

SCE functions with peaks displaced from the pupil center have also occasionally been measured for presumably normal observers (Flamant and Stiles, 1948; Westheimer, 1968; Wijngaard and van Kruysbergen, 1975). The literature cited above suggests that anomalous or displaced SCE functions may more often be found in amblyopic than in nonamblyopic eyes. Unfortunately, the samples of both amblyopic and nonamblyopic eyes are rather small. Moreover, observer alignment and centration within the testing instrument was not adequately monitored in all of these studies. It is presently not clear to what extent visual acuities are affected in normal eyes having displaced SCE function peaks. Evidence which bears upon this question is presented in Chapter VII.

On logical grounds, disturbed receptor orientation could degrade visual resolution in several ways (Enoch, 1957; 1959a, b; 1967a): (1) a decrease in brightness of the resolution target because of the SCE, (2) a locally effective meridional increase of the retinal receptor mosaic dimension for sheered over receptors, (3) light leakage or cross-talk between neighboring receptors (Enoch, 1960),

(4) reduced contrast because of increased scattering from the receptors, and (5) increased sensitivity to stray light within the eye, also reducing contrast. As discussed in the last chapter, in vitro studies of the optical properties of both animal and human receptors confirm that poorly oriented receptors are poorer light collectors and have poorer optical transfer capabilities than well oriented receptors. The evidence (see Chapter II) suggests that a modest amount of "tilt" of the receptors, in which orientation within groups of receptors is maintained, but the overall alignment tendency is toward a noncentral region of the exit pupil, should entail a lesser degradation of retinal resolution capability than malorientation in which there is a loss of alignment between neighboring receptors.

However, hypothesized photoreceptor alignment anomalies within amblyopic eyes might contribute to amblyopia other than by a direct degradation of resolution. For example, some amblyopic subjects report that stimuli viewed with the amblyopic eye appear less bright than when viewed with the fellow, nonamblyopic eye (Grosvenor, 1957; Burian, 1967b; Flynn et al., 1971; Bedell, 1974). These results are qualitatively consistent with the presence of certain forms of anomalous receptor alignment. In particular, alignment of the receptors toward a significantly decentered region of the dilated pupil would be expected to cause a reduction of the apparent brightness of stimuli viewed with the natural pupil.*

*Such a mechanism could be implicated in the suppression of the amblyopic eye under conditions of "binocular" viewing, for example.

However, quantitative data for such a relationship are lacking. Moreover, the reduction of perceived brightness in these amblyopic eyes might well be attributable to changes at a site or sites other than at the photoreceptor.

CHAPTER IV
DEFINITION OF THE PROBLEM

The receptor alignment anomalies, inferred from SCE function measurements, which occur in some amblyopic eyes, represent the first level in these amblyopic visual systems at which a discrete pathology is indicated.* The contribution of such anomalies to the status of visual functioning in affected amblyopic eyes therefore warrants extensive investigation. The extent to which such anomalies occur in amblyopic eyes as well as in nonamblyopic and presumably normal eyes also requires clarification.

In the past, the assessment of receptor orientation in amblyopic eyes has been confined to the fixation area (Enoch, 1957, 1959a, b; Marshall and Flom, 1970; Dunnewold, 1964) or to a small region around it (Bedell, 1974). Since the SCE function peaks of normal observers have been shown to cluster near the center of the pupil when measured up to 35° in the peripheral field, it seemed reasonable to ask whether the evidence of photoreceptor malorientation found in some amblyopic eyes at fixation also exists at other retinal loci.

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*The visual resolution reduction caused by preretinal media anomalies and pathology is not here categorized as amblyopia. See footnote, Chapter I.

In particular, since the visual functioning of amblyopic eyes apparently tends to approach that of normal eyes in the amblyopic eye peripheral visual field, it seemed appropriate to investigate whether receptor orientation conforms to this same trend. That is, it was sought to determine whether, in those amblyopic eyes in which receptor orientation anomalies could be demonstrated, such anomalies were confined to a central retinal area in which acuity deficits were found. Alternatively, receptor orientation anomalies might extend beyond the region of visual acuity impairment and characterize such retinae as a whole.

This research, then, sought to utilize the psychophysical SCE function to characterize the nature of possible receptor orientation anomalies within the eyes of functional amblyopic observers at several locations spanning the central and near peripheral retina. Since the number of investigations which have examined the SCE function in amblyopic eyes is small, this research, even though limited in its sample size, was also expected to contribute to the question of the extent to which receptor alignment anomalies occur in functional amblyopic eyes exhibiting limited visual decrements.

As discussed in the Introduction, the pattern of inferred receptor alignment across central and near peripheral retinal locations in amblyopic eyes might be expected to provide information concerning the nature of the hypothesized mechanisms controlling such alignment as well. In order for a precise control of receptor alignment to occur, a signal (or signals)

must exist, based upon which departures from correct alignment are determined. Thus, receptor alignment mechanisms presumably contain both afferent, error-signal-detecting, and efferent, receptor-alignment-correcting, components. Various forms of receptor alignment anomalies might reflect disturbances of either of these components or of the alignment signal itself.

Thus, if amblyopic eyes were identified, in which the inferred receptor orientation across a wide retinal area indicated that receptors converged toward an anomalous alignment centrum, displaced from the pupil center, then a global or retina-wide disturbance of alignment mechanisms within such eyes might be entertained. One might hypothesize that the alignment signal, or its detection, was altered in such cases. Were evidence of gross receptor malorientation found at all sampled retinal locations, a global disturbance of the alignment mechanism, probably of a different sort, would be indicated. On the other hand, were evidence of receptor alignment anomalies found only within circumscribed retinal regions, and evidence of normal alignment toward the central area of the exit pupil found elsewhere on the same retina, then a local disturbance of receptor alignment mechanisms, and not of the alignment signal, might reasonably be inferred. Having identified retinal regions or entire eyes in which receptor orientation, and presumably receptor alignment mechanisms, were apparently disturbed, then subsequent studies might attempt to identify electrophysiological, metabolic,

biochemical or other anomalies within such retinal regions or eyes which correlated with the apparent malfunctioning of the hypothesized receptor alignment mechanisms.

Thus, one of the aims of this dissertation research was to identify individuals in whom receptor alignment anomalies existed and to characterize such anomalies with respect to location on the retina. Subsequent investigations of the eyes of such individuals could then reasonably be directed toward understanding the nature of hypothesized receptor alignment mechanisms.

CHAPTER V
OBSERVERS AND EVALUATION

Observers

Amblyopic and nonamblyopic control observers were solicited from the University of Florida campus and J. Hillis Miller Health Center populations by means of posted advertisements and by word of mouth. None of the observers of this study were referred directly from clinical sources. Potential observers were screened for possible amblyopia with a portion of the clinical evaluation described below (history, monocular visual acuities for Landolt targets, cross cover test, entoptic projection of the fovea). Informed consent was obtained in writing from observers agreeing to participate in the study. The observers were compensated for time spent on the project.

One of the control observers (SBS) had participated in a previous SCE function study (Bedell and Enoch, 1978). All other observers were naive to visual psychophysical measurements.

Evaluation

Both the amblyopic and nonamblyopic observers were evaluated with the same program of clinical tests. These

included (1) a history, (2) best corrected and pinhole visual acuities for Landolt targets, (3) refractive status assessed by retinoscopy, (4) strabismus/binocularity/motility examination, (5) ocular tensions, and (6) slit lamp and ophthalmoscopic evaluation of the eyes.

History

The following information was obtained from potential amblyopic observers: (1) age of onset of amblyopia, (2) circumstances surrounding onset, (3) treatments and attending physicians, (4) presence of reduced vision or strabismus along relatives, and (5) present visual status. The last item inquired as to the observer's subjective impressions concerning monocular and "binocular" vision under everyday circumstances.

All observers were asked about any personal or family history of eye disease, and specifically whether there was a history of glaucoma or of ocular hypertension. Observers were asked to give known drug reactions and to describe their last visit to an eye care professional, including whether dilation was performed at that time. This portion of the history was intended to elicit information concerning possible contraindictions for dilation of the eyes. Dilation was deemed necessary for the SCE function measurements.

Visual Acuities

Monocular visual acuities for 8 position double break Landolt C targets were obtained with best correction. Targets

were presented on a commercial chart (Bausch and Lomb, Rochester, N. Y.) viewed at 20 ft. Chart luminance was 1.93 log cd/m^2 provided by white fluorescent lighting. Target contrast was approximately 80 per cent.* Acuities were checked for improvement with a pinhole placed over the observer's correction.

Refractive Status

Visual corrections were initially estimated from lensometer readings of observers' spectacle correction, if any. Additionally, retinoscopy was performed on all observers at the locus of fixation, in most cases by Dr. Jay Enoch. Dr. Enoch or the author performed retinoscopy for peripheral visual field test locations in order to estimate the lens corrections necessary for SCE function testing at these locations.

Strabismus/Binocularity/Motility Examination

In most instances, the strabismus examination was performed by the author. The cross cover test was used to screen for tropia (misalignment of the visual axes of the two eyes under "binocular" viewing conditions) on the initial visit to the laboratory. When a positive result was found, the prism necessary to neutralize the deviation on the cover test was determined. Tropias were evaluated both at far and

*$\text{Contrast} = \frac{\text{Chart luminance} - \text{Target luminance}}{\text{Chart luminance} + \text{Target luminance}}$

at near, with correction, and in up and down gaze to determine A or V pattern of any deviation. A 9 gaze position muscle field screened for incomitant deviations. Lateral phorias in orthotropic observers were evaluated at both far and near by finding the prism necessary to vertically align a target seen in binocular diplopia as the result of a 6 diopter vertical prism placed before one eye.

Retinal correspondence under "binocular" viewing conditions was assessed by the afterimage and striated glasses tests. In the former, horizontal and vertical line afterimages were formed respectively in the nonamblyopic and amblyopic eyes of amblyopic observers, by sequential monocular inspection of appropriately oriented illuminated slits. There was no preferential order of afterimage formation for the control observers. Under "binocular" viewing conditions and in the absence of monocular eccentric fixation, alignment of the centers of the horizontal and vertical afterimages, to form a cross, indicates normal retinal correspondence. Misalignment of the afterimage centers is indicative of an anomalous retinal correspondence.

The striated glasses test was performed with Bagolini striated lenses (House of Vision, Chicago) placed obliquely at 45° and at 135° before the right and left eyes respectively. Intersection of the streaks, formed by the lenses over each eye, at a small, illuminated fixation target is indicative of anomalous retinal correspondence in heterotropic observers. Misalignment of the streaks equivalent

to the angle of deviation indicates a normal retinal correspondence.

The afterimage test was conducted at far and the striated lenses test at both far and near. Disagreement between the two tests in heterotropic individuals is not uncommon, apparently because of the more dissociating (less like normal seeing conditions) aspects of the afterimage test (Bagolini, 1976).

Monocular fixation positions were estimated using one or more of three entoptic techniques (c.f. Moses, 1970). These were the location of the Maxwell spot centroid with respect to a fixation target, the location of the Haidinger brush with respect to a fixation target and the location of the avascular zone of the entoptic Purkinje retinal vessel pattern with respect to a fixation target. All measurements were converted to units of visual angle.

The Maxwell spot is a pinkish or lighter splotch of color seen within a purple field (other colors of Maxwell spots are seen against other color fields). The spot subtends about 2° for most individuals and apparently results from the selective absorption of short wavelength light by the macular pigments. In many individuals, substructure is evident in the spot. Observers viewed the Maxwell spot monocularly on an alternately purple and neutral (Edmund Roscolene filter #827 + #846 for purple, #883 for neutral) fluorescent back-lighted screen of 1.4 log cd/m^2, measured with filters in place. Alternating purple and neutral lights

were employed to avoid fading of the spot. The observer localized the centroid of the spot with respect to a black fixation target by superimposing a movable and adjustably-sized circular cursor light upon the Maxwell spot while fixating the target (Kandel and Bedell, 1972).

The Haidinger brush is another entoptic phenomenon also apparently related to the macular pigment and in particular to its presumed dichroic absorption characteristics. In bluish light, the brush is seen as a propellor shaped object through a linear polarizer. If the polarizer is rotated, the propellor appears to spin. Using a movable cursor light, the axis of rotation of the propellor may be located with respect to a fixation target. This test was performed using the same equipment as for the Maxwell spot test, but substituting a blue (Wratten #34) filter and rotating linear polarizer for the alternating purple and neutral filters. Screen luminance was 0.6 log cd/m^2 under the actual viewing conditions.

The shadows of the retinal blood vessels may become apparent when the angle of the incident light upon the retina is changed, causing the vessel shadows to move. Since the foveal region is characterized by the absence of capillary support from the inner retinal circulation, it appears as a "hole" in the entoptically viewed retinal vessel pattern. Purkinje retinal vessel patterns were generated by rotating an eccentrically located 1.8 mm diameter pinhole in front of the dilated eye (Boer and Hofstetter, 1972). The observer viewed a 3.1 log cd/m^2 luminance white screen through the

rotating pinhole. The avascular region of the vessel pattern was located with respect to a fixation target using a cursor light.

Vessel patterns could also be generated within the SCE testing apparatus (see Chapter VI). In this way SCE function and interferometric visual resolution targets could be assured to be centered within the avascular region.

Binocularity was evaluated using three separate tests. The first of these was the Titmus vectograph test which presents a series of graded horizontal disparity targets, seen in depth by binocularly normal individuals, through polaroid lenses (Titmus Optical Co., Inc., Petersburg, Va.). This test has been critized because of the presence of many monocular cues in the design. Binocularity was also assessed by the ability to appreciate the Pulfrich stereophenomenon, which is the appearance of depth in the orbit of a swinging pendulum viewed binocularly, but with a neutral filter over one eye (c.f. Gregory, 1973). Finally, observers were presented with pairs of random dot stereograms (Julesz, 1971) in a Clement Clarke synoptophore. Targets had a horizontal disparity of approximately 600 sec of arc. Binocularly normal individuals appreciated a figure or figures either above or below the plane of the target background when stereogram half-pairs presented to each eye were brought into register. No figure is available in either stereogram half-pair alone.

In addition to the above examinations, observer SSD was referred to Dr. Matthew Rabinowicz of the Opthalmology Department, J. Hillis Miller Health Center for further strabmismological evaluation.

Tension and Slit Lamp, Ophthalmoscope Examination

Intraocular pressures were measured using applanation tonometry at the time of the slit lamp and ophthalmoscopic examinations. These examinations were performed by Dr. Constance R. Fitzgerald, of the Department of Ophthalmology, J. Hillis Miller Health Center. Slit lamp examination assessed the cornea, anterior chamber, lens and anterior vitreous body. In particular, the examination sought small opacities in the optical media which might interfere with SCE function measurements. Gonioscopy was performed to evaluate the depth of the angle between the iris and limbus. An ophthalmoscopic examination of the fundus was performed in order to rule out observable pathology in amblyopic (and nonamblyopic eyes) as a cause for possible anomalous SCE functions.

Selection Criterion

Amblyopic observers were expected to have a difference of one line or more in their best corrected, monocular visual acuities for Landolt ring targets. The acuity deficits were expected to be of long standing, i.e., dating to childhood, as revealed by the history. Furthermore, some contributory history of strabismus, anisometropia or early abnormal visual experience was anticipated. Anterior chamber and fundus

examinations were expected to reveal no abnormalities which might be responsible for the acuity findings. All amblyopic observers met these criteria. The results of the clinical examinations of the amblyopic observers are summarized in Appendix A.

Control observers were expected to have at least 20/20 best corrected monocular visual acuities for Landolt targets in each eye and minimal between eye acuity differences. Anterior chamber and fundus examinations were expected to reveal no abnormalities. The control observers were also expected to be orthotropic. Observers SBS and MAP met these criteria. Observer JEC, who was originally recruited to be a control observer, revealed possible fundus abnormalities within both eyes on the ophthalmoscopic examination. The pattern of SCE functions measured in both eyes of this observer also departed from results obtained for other control observers. Thus, observer JEC will be treated as a special case. The results of the clinical evaluations of JEC and of the control observers are presented in Appendix B.

CHAPTER VI
APPARATUS AND PROCEDURES

SCE Apparatus and Testing Procedures

The instrument used to determine SCE functions appears schematically in Fig. 1. A cube beam splitter (BS1) divides the collimated beam (lens LO) from a tungsten ribbon filament source (S) into test (A) and surround (B) beam channels. Within both channels, the ribbon filament is imaged by lenses L1A and L1B at four times lateral magnification onto approximately 0.30 mm diameter round apertures (APA, APB), mounted on mechanical stages, which serve as secondary sources. A portion of the beam in channel B is diverted by a pellicle (PL) and falls on a photovoltaic cell (V) the output of which is monitored. The apertures are collimated by lenses L2A and L2B and channels A and B are rejoined at a second beam splitting cube (BS2), after passing through adjustable field stops (FSA, FSB). After passing through beam splitter BS3, lens L3 forms unit lateral magnification images of apertures APA and APB in the observer's entrance pupil (EP). Movement of either aperture by means of its mechanical stage mounting causes an equal and opposite movement of its image in the entrance pupil. The filament images were found to be homogeneous to 0.10 log unit through 7 mm

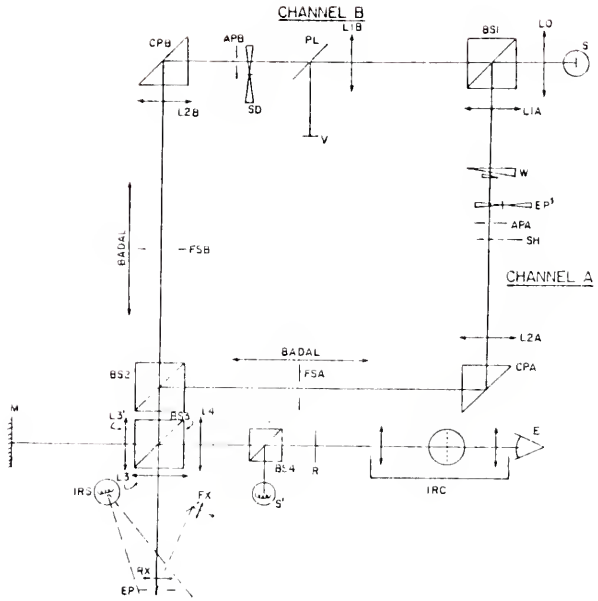

FIGURE 1

Schematic Diagram of Stiles-Crawford Function Apparatus

horizontally and to less than 0.10 log unit through 8 mm vertically.

At BS3, a portion of both test and surround field beams are deflected and imaged by lens L3' onto a first surface mirror conjugate with the observer's entrance pupil. Reflected images pass backward through lens L3' and join infrared radiation reflected from the observer's eye, provided by tungsten infrared sources (IRS), at cube BS3. Lens L4 forms an image of the test and surround field beams and of the observer's pupil on a reticle (R), marked in concentric circles. The reticle is retroilluminated by infrared source S' reflected in cube beam splitter BS4. The reticle and images of the entrance pupil and both the test and the surround field beams as they enter the pupil are viewed by the experimenter (E) in an infrared image converter system (IRC, RCA #6914A).

Provision for filtering of both test and surround field beams is made in the collimated portions prior to lenses L1A and L1B. The test field beam passes through a Kodak neutral wedge and balance filter (W) and is interrupted twice per second by an episcotister (EP'). Calibrations of the wedge and neutral filters were carried out in situ and with chromatic filters in place using a model 1980 Spectra Pritchard photometer (Photo Research, Burbank, Ca.) fitted with a 40X objective attachment and placed at EP. Calibrations were verified, also using the Pritchard photometer, by the method of Westheimer (1966) for Maxwellian view systems.

Field stops FSA and FSB are adjustable toward and away from lens L3, thereby functioning as Badal optometer systems with a range of approximately 2.0 diopters. Supplemental lens corrections, based on retinoscopic examination, could be placed (at RX) close to the observer's eye. Vertex distances were carefully measured and corrections centered on the optical axis of the system. A correction for the spectacle RX was applied to the displacements of the surround beam in the entrance pupil. For data taken at other than fixation, the observer's gaze was directed to a dim red collimated fixation source (FX). At the locus of fixation, the centered test array itself served as a fixation target.

The observer was held in position by means of a dental impression and forehead rest, both attached to a frame which is adjustable in the x, y, z directions. The experimenter positioned the observer using these controls, while observing the image of his entrance pupil upon the reticle in the IR image converter. Pupil position was monitored continuously and adjusted during experiments to maintain proper alignment with respect to the test and surround field beams and the exit pupil plane of the instrument.

Observers' eyes were dilated with 10 per cent phenylephrine hydrochloride (Neo-Synephrine) or 1 per cent tropicamide (Mydriacyl) after ruling out ocular pathology. Photopic SCE functions were determined by an increment threshold procedure, the test beam being fixed at the pupillary center and the surround beam displaced in successive steps across the pupillary

aperture. The observer viewed a 0.50° test field limited by aperture FSA, superimposed upon the center of a larger (4°24') surround field defined by FSB. Since both FSA and FSB are mounted on mechanical stages, aperture FSB could be shifted to compensate for changes in position of its retinal image, as the result of occular aberrations, when the surround beam was displaced from the pupillary center. The test and surround fields were thereby maintained in concentric alignment for all pupil entry positions of the surround field beam.

Discounting the SCE function itself, background field luminance was 3.04 log photopic trolands (1100 trolands). Both test and surround fields were orange (Kodak Wratten #23A filter). Increment thresholds with both test and surround beams at the pupil center were determined over a 4 log unit range at each visual field test location for each observer. The increment threshold data indicated that all SCE tests were conducted on the Weber portion of the increment threshold curve (see Chapter II, also Enoch and Hope, 1972a, Appendix 2).

SCE functions were determined at a number of visual field locations spanning central and near peripheral retinal positions. The test locations chosen were (1) the locus of fixation, (2) the fovea, if different from (1), (3) 5° nasal visual field (NVF), (4) 10° NVF, (5) 20° NVF, (6) 5° temporal visual field (TVF), and (7) 10° TVF. All visual field testing locations were not examined for all observers. For some

observers, SCE functions were determined at test locations in addition to those listed above.

In order to determine whether testing at the fixation locus also included the fovea, the Purkinje retinal vessel pattern was generated within the SCE testing apparatus. In this way, the entoptically viewed avascular zone of the vessel pattern could be located with respect to the test field under the actual testing conditions. A 2 diopter prism, placed between aperture APB and lens L2B was rotated by a variable speed motor, causing the image of APB to rotate through a circle of approximately 2 mm radius in the observer's entrance pupil. Observers who could appreciate the pattern saw a slightly wobbling retinal vessel pattern within the surround field and noted, when fixating the test field, whether the avascular zone of the vessel pattern was concentric about the test field. If not, the observer located a variable position fixation target, produced by back reflection of an attenuated laser beam from the rear surface of field stop FSA, in the position which brought the avascular area of the vessel pattern to surround the test field. Distance between the fixation light and the center of the test aperture was determined by micrometer and converted to visual angle. "Foveal" SCE functions were determined with the observer fixating either this laser fixation target or one of the movable collimated fixation sources (FX) placed at the appropriate location.

All thresholds were determined by the method of adjustment, with the stipulation that the observer always approached the endpoint from the same direction, i.e., either ascending or descending. Between endpoint determinations, the experimenter randomly disturbed the wedge setting by up to 0.6 log units in either direction. Data were collected with both the increment and surround field beams first entering at the pupil center. Endpoints were then determined for pupil entry positions of the background field beam displaced in steps along one pupil half meridian, and subsequently along the opposite half meridian. Periodically, thresholds with both beams entering at the pupil center were redetermined, in order to provide a baseline of possible observer changes in criterion or sensitivity during testing. Typically, both horizontal and vertical traverses of the pupil were completed for a single visual field test location for one eye in one session. Observers were first tested at the locus of fixation; testing at the most peripheral visual field locations was typically reserved for the last sessions. Otherwise there was no particular order of testing. Right and left eyes were tested more or less alternately across sessions.

Raw SCE function data were in the form log (wedge plus filter) neutral densities (ND) attenuating test field luminance at threshold, determined at a number of pupil entry positions of the surround field beam. Based upon the argument presented in Chapter II, log ND values are equivalent to $-\log \eta$. The raw data for each meridian were thus computer

fit to a least squares regression equation based upon the parabolic equation proposed by Stiles (1937, see Chapter II). The equation used was

$$y = b_1 + b_2x + b_3x^2$$

in which ND is represented as y and pupil entry position of the surround beam as x. Functions of the fitted constants b_1, b_2, b_3 define the shape factor rho (ρ), the location of the function peak, and the ND value at the peak. SCE function peak locations for a single meridian were estimated from the ratio $-b_2/2b_3$. The SCE function peak location within the pupil for each visual field test location was estimated by vectorially summing the estimated peak displacements from the pupil center along the horizontal and vertical test meridians. Two indices of directionality were derived. The first of these was Stiles (1937) rho value, which is estimated by the parameter b_3. Additionally, half sensitivity half widths in mm (Enoch and Bedell, 1978) were derived from the fitted functions.

The best fitting parabola was found using all data, unweighted by position, within 3 mm of the function peak. It has been repeatedly noted that SCE function data more than 3 mm from the function peak are no longer well fit by a parabola (Stiles, 1937; Safir and Hyams, 1969; Safir et al., 1971; Enoch and Bedell, 1978). Pupil entry position data (x values) were adjusted for beam displacements resulting from the use of spectacle lenses within the SCE apparatus. Additionally, since the pupil appears foreshortened when

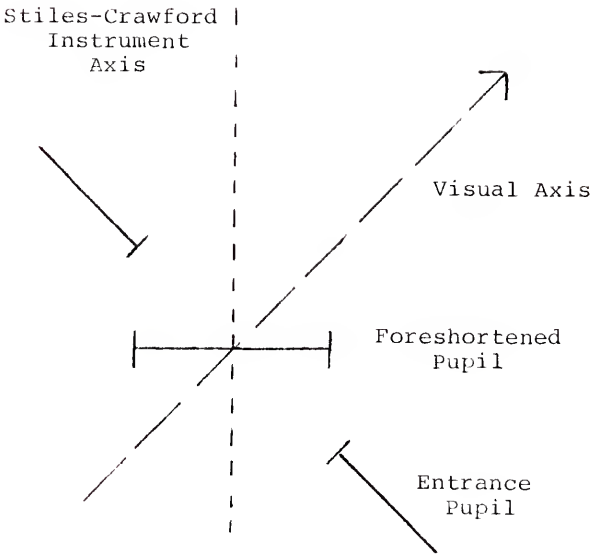

FIGURE 2

Relationship Between Stiles-Crawford Function Apparatus
Exit Pupil and Observer's Entrance Pupil
During Peripheral Visual Field Testing

viewed obliquely, corrections were made in the meridian of foreshortening when testing was 15° or more in the peripheral visual field (see Fig. 2). Thus, for example, when testing at 20° in the nasal visual field, a correction of $(\cos 20°)^{-1}$ was applied to horizontal surround beam pupil entry positions; in this case, no correction is required for vertical displacements. At less than 10° obliquity, the cosine correction is insignificant. Finally, on some occasions, and generally for peripheral visual field test locations, threshold NDs were corrected for changes in observer sensitivity or criterion which occurred during the session. Corrections were determined by interpolation between the estimations of increment threshold with both beams entering at the pupil center which were taken periodically during the testing session.

Interferometric Resolution Testing Apparatus and Procedures

Visual resolution was measured for grating targets formed by a two beam interference pattern. The interferometric resolution device, shown in Fig. 3, is folded into the SCE testing apparatus. A 2 mW helium-neon gas laser beam is imaged by a 10X microscope objective (OB). This image is doubled by a Wollaston prism (W) sandwiched between two linear polarizers (POL), with axes at 45° to the prism's ordinary and extraordinary axes. This arrangement results in two diverging beams emerging from the prism with the same polarization, hence maximizing interference and fringe

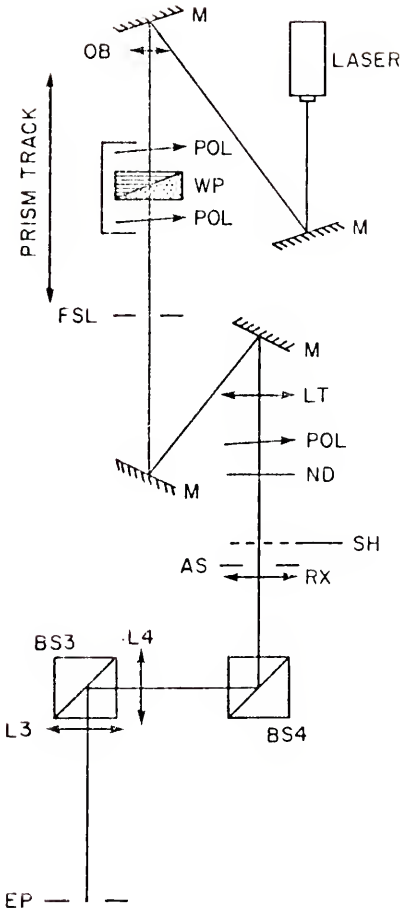

FIGURE 3

Schematic Diagram of Interferometric Resolution Apparatus

contrast. Variation of beam separation at the observer's entrance pupil, and thereby of grating spatial frequency, is achieved by displacement of the Wollaston prism and polarizer sandwich along a track parallel to the optical axis of the system. The position of the prism on the track is indicated on a digital meter, scaled in decimal acuity,* as the voltage through a multiple turn linear potentiometer having its shaft attached to the sprocket drive of the prism carrier. Rotation of the prism and polarizer sandwich rotates the meridian of beam doubling and hence of grating orientation.

A +2.50 diopter trial lens (LT) images the doubled laser image at -0.33 lateral magnification at an aperture stop (AS) conjugate with the entrance pupil of the observer's eye (EP). Beams are imaged symmetrically about the center of the observer's entrance pupil by Maxwellian view lens L3 after entering the SCE apparatus at BS4 and collimation by lens L4. As for SCE function determinations, the observer's pupil position relative to the exit pupil of the instrument is monitored using the IR image converter system.

A field stop for the grating target is provided at FSL at the end of the prism carriage. This stop is imaged by LT at approximately the position of BS4 and reimaged by lenses L4 and L3 to appear at infinity to an emmetropic observer at EP. Lens corrections (RX), if required, are centered

*Decimal acuity = 1/(target detail, in minutes of arc visual angle).

on the optical axis of the system at the aperture stop, AS, and are therefore conjugate with the observer's entrance pupil. Hence, corrective lenses at AS alter beam separation, and therefore grating spatial frequency,* only minimally. Corrective lenses at AS also slightly change the magnification of field stop, FS, and hence slightly increase or decrease the visual angle subtended by the grating target. For the lens powers used, changes in target diameter were much less than 10 per cent and are considered to be negligible.

Beam separation within the entrance pupil is related to grating spatial frequency according to the relation

$$\text{spatial frequency} \propto \text{beam separation/wavelength}$$

Hence, larger beam separations with the pupil correspond to higher spatial frequency grating targets.

As beam separations within the entrance pupil become larger, ca, 1-1/2 - 2 mm, the resolution channel acts like a Scheiner optometer. Thus, the images of FSL provided by the two interfering beams are exactly in register only when the observer is emmetropic for the meridian defined by beam separation in the pupil. In the presence of refractive error in the meridian of beam separation, a doubling of the grating target is observed. Target doubling occurs perpendicularly to the grating orientation and is therefore a potential cue to grating orientation in the absence of resolvable detail.

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*Spatial frequency = number of bright and dark line pairs per degree of visual angle.

When refractive error is present, target doubling tends to increase as beam separation in the pupil increases and therefore as grating spatial frequency increases.

For this reason, considerable care was taken to eliminate apparent doubling of the grating targets. This was achieved by finding the appropriate lens which, when placed at AS, completely eliminated doubling of the target for the maximum beam separation within the entrance pupil. Spherical aberration of the eye was considered negligible for beam separations of 2 mm and less.

Grating targets were presented at two orthogonal orientations. Because visual astigmatic axes are most often either with or against "the rule," i.e., greatest refractive power either along a horizontal or vertical axis, and much less commonly oblique, grating targets were presented at 45° and 135° (up right and up left), in order that the meridian of beam separation in the pupil would straddle the expected horizontal or vertical astigmatic axis. In such cases, refractive correction for both target orientations was possible with a single spherical lens.

Due to polarization effects caused by multiple reflections, the complexity of the beam doubling system or asymmetries in the laser output, the energy passed by the optical system for 45° grating orientations was approximately 0.3 log units more than that passed for gratings oriented at 135°. A linear polarizer (POL), placed at 35° from the vertical between lens LT and AS equalized the luminance of gratings

at both orientations at 3.66 log photopic trolands (4570 trolands). Neutral filters (Tiffin), were placed in the interfering beams to attenuate acuity field luminance in steps. Filters were calibrated both within the instrument using laser light, using the Spectra Pritchard photometer, and with a Beckman Acta III recording spectophotometer at wavelength 632.8 nm, corresponding to the wavelength of laser output. Components were oriented in the beams so as to avoid spurious interference patterns from multiple reflections.

Grating resolution targets were presented as a 1° circular field against a 4°24' surround field provided by channel A of the SCE instrument (Fig. 1). A 0.50° resolution target was also presented for foveal measurements. The surround field was filtered by a Kodak Wratten 29 filter, which provided red light with a dominant wavelength of 632.7 nm in illuminant C (approximated by the tungsten source used), according to Kodak specifications. Resolution field contrast was 0.80 without a background field; the background reduced contrast to 0.71.* Equal logarithmic reductions of resolution

---

*Contrast = $\frac{L_b - L_d}{L_b + L_d}$

Adding a background increases both light and dark line luminance equally. Thus,

$$\text{Contrast} = \frac{(L_b + L_s) - (L_d + L_s)}{(L_b + L_s) + (L_d + L_s)} = \frac{L_b - L_d}{L_b + L_d + 2L_s}$$

where L_b = luminance of bright lines,

L_d = luminance of dark lines, and

L_s = luminance of surround field

target and surround field luminances maintained a constant contrast at all luminances tested.

The resolution target was exposed for 250 msec once each 5 sec at the center of the surround field. A solenoid shutter (SH) at AS and a Hunter timer triggered by a synchronous motor controlled exposure periods. The surround field was presented continuously.

Resolution thresholds were estimated by a criterion independent adapted psychophysics procedure (Kelley and Savoie, 1973; Bedell and Enoch, 1978). In this procedure the observer is required to make a two alternative forced choice decision following each target exposure, i.e., grating target oriented with lines up right or up left. Gratings were presented at 45° and 135° in a pseudorandomized order and beginning at a low spatial frequency. Following correct responses, the grating spatial frequency was increased in steps until the observer made his first error. Target spatial frequency was then reduced. Thereafter, spatial frequency was reduced following each error and increased following two successive correct identification of orientation. In this way a threshold corresponding to 71 per cent correct is tracked over time.*

---

*A threshold corresponding to 71 per cent is derived as follows:

> At threshold, the probability that the experimenter increases target spatial frequency equals the probability that he decreases target spatial frequency. If P (correct) = p, then (cont.)

Data analysis consisted of finding the average resolution target spatial frequency half period (i.e., the dark line width), in minutes of arc, at which reversals from increasing to decreasing spatial frequency or vice versa occurred. Minute of arc values were calculated reciprocals of the equivalent decimal acuities, recorded by feeding voltmeter signals to a Fisher Recordall strip chart recorder. The first reversal was always discounted, since decision strategy for it corresponded to a 50 per cent rather than 71 per cent correct threshold. The first reversal served to find the appropriate region within which thresholds might be tracked.

The resolution device did not produce lines finer than 0.57 minutes of arc half period (decimal acuity = 1.76). When observers correctly identified grating orientation at spatial frequencies of 0.57 minutes of arc, resolution threshold was estimated as the average grating spatial frequency half period at which the observer tracked during the testing interval. Such thresholds were pinned on the high side and must be treated as

---

P (decrease spatial frequency) = P (correct twice successively) = $p \cdot p = p^2$

P (increase spatial frequency) = P (not correct twice successively) = $1 - p^2$

Since P (decreases spatial frequency) = P (increase spatial frequency)

or $p^2 = 1 - p^2$

$p^2 = 1/2$, $p = 0.707$

conservative. No observer tracked at the acuity limit for all foveal testing conditions. Moreover, observers tended to perform more poorly when the 0.50° rather than 1° foveal target was used. Assuming Weber's law to be valid in this instance, a discrimination based upon possible target doubling rather than upon grating detail should have been more easily performed for the smaller than for the larger targets. These data indicate that the observers based their discriminations upon grating detail rather than upon doubling of the target. Additionally, the observer (BAJ) who consistently tracked at the maximum spatial frequency value for foveally presented 1° targets failed to discriminate the orientation of possible target doubling at the maximum beam separation in the pupil in a two alternative forced choice situation.

Interferometric grating resolution thresholds were determined at at least five visual field locations and for three luminances of the grating target and surround. Grating test luminances were -0.5, -1.5, and -2.5 log units decreased from the maximum target luminance of 3.66 log photopic trolands (4570 trolands). The corresponding surround luminances were 2.23 log photopic trolands (170 trolands) and -1 and -2 log units reduced from this value. For observer JEC only, resolution thresholds were determined foveally with grating luminance at -3.5 log units and surround luminance at -3 log units from maximum levels.

The visual field test locations examined were the locus of fixation, 5° nasal visual field (NVF), 10° NVF, 5° temporal

visual field (TVF) and 10° TVF. When there was evidence that fixation was not at the foveal center, resolution thresholds were determined for 0.50° grating targets placed at the foveal center as determined entoptically using the retinal vessel pattern generated within the SCE instrument. For the amblyopic eye of observer JEM, resolution thresholds were determined at 5° and 10° on either side of the estimated foveal location, rather than at 5° and 10° in the nasal and temporal visual fields.

Resolution thresholds for all test locations and luminance levels were determined for one eye of an observer in a single session. Thresholds for the second eye were determined on another day. With the exception of observer PMC, the nonamblyopic, fellow eyes of the amblyopic observers were tested first, in order that any practice effects would benefit the amblyopic eyes.

CHAPTER VII
RESULTS

Stiles-Crawford Effect (SCE) Function Peak Locations

Control Observers

The estimated SCE function peak locations for visual field test locations between 10° temporal visual field (TVF) and 20° nasal visual field (NVF) are shown for both eyes of the control observers, SBS and MAP, in Figs. 4 and 5. The estimated SCE function peak location for a test area 35° in the TVF of observer SBS's left eye, replotted from Bedell and Enoch (1978), is also shown in Fig. 4.

The plotted SCE function peak locations in Figs. 4 and 5, as well as in subsequent Figs. 6 - 12, represent the combined estimates of SCE function peak displacements from the pupil center for horizontal and vertical traverses of the pupil, at the visual field location tested. That is, considering the pupil as a Cartesian coordinate plane, the estimated SCE function peak locations within the pupil plane were determined as the coordinate location corresponding to the estimated horizontal (temporal-nasal, x axis) and vertical (superior-inferior, y axis) peak displacements from the pupil center. When multiple estimates of the SCE function peak location were determined for a single visual

field test location, the location plotted in the figures represents the averages of the estimated horizontal and vertical locations.

Estimated SCE function peak locations for single horizontal and vertical traverses of the pupil are tabulated for the control observers in Appendix C. As an aid in rounding, tabulated values have been carried to an extra decimal place. In addition, for both the horizontal and vertical pupillary meridians, confidence intervals, having a 99 per cent probability of containing the true function peak, were calculated from regression statistics (Williams, 1959). The 99 per cent confidence intervals for vertical and horizontal locations of the peak permit the definition of a confidence rectangle having a 98 per cent probability* of containing the true peak. When confidence rectangles for two SCE function peak locations do not overlap, the true peaks may be concluded to differ in location with a minimum confidence of 96 per cent** (Hays, 1963). The computational formula for 99 per cent confidence intervals and the definition of the confidence rectangles are provided at the end of Appendix C.

Inspection of Figs. 4 and 5 reveals that the estimated SCE function peak locations for both eyes of the two control observers, for test positions spanning 30° of the

---

*(.99) x (.99)

**(.98) x (.98)

horizontal meridian of the visual field, in all cases cluster within a small area near the center of the pupil. When considering these figures, it is useful to recall that 1 mm in the entrance pupil corresponds to approximately 2.5° at the retina (O'Brien, 1946; Bedell and Enoch, 1978). The results shown here are similar to those reported by Enoch and Hope (1972a) for one eye of each of three observers tested over the same range of visual field locations, and to the results of one eye of each of four additional observers tested over only a part of this range (Enoch and Hope, 1973).

A comparison of the pattern of estimated SCE function peak locations within the two eyes of each control observer reveals very little difference in clustering tendency between the eyes. Between eye differences in clustering of the SCE function peaks for this range of visual field testing locations is further considered below.

Amblyopic Observers

Clearly anomalous SCE functions were not identified within any of the sample of amblyopic eyes studied at any of the visual field test locations. All amblyopic eye SCE functions had estimated peaks falling well within the dilated pupil. Moreover, all of these amblyopic eye SCE functions were well fit within 3 mm on either side of the estimated peak location by parabolas. The amblyopic sample tested is defined in Chapter V and in Appendix A.

FIGURES 4 - 12

Estimated Locations of SCE Function Peaks
at Several Visual Field Testing Locations
for Control and Amblyopic Observers

Key

a 35° Temporal Visual Field (TVF)

b 25° TVF

c 10° TVF

d 5° TVF

e Fixation

f "Fovea" (see Appendix C)

g 2-1/2° Nasal Visual Field (NVF)

h 5° NVF

i 7° NVF

j 10° NVF

k 15° NVF

l 20° NVF

o 10° Inferior Visual Field (IVF)

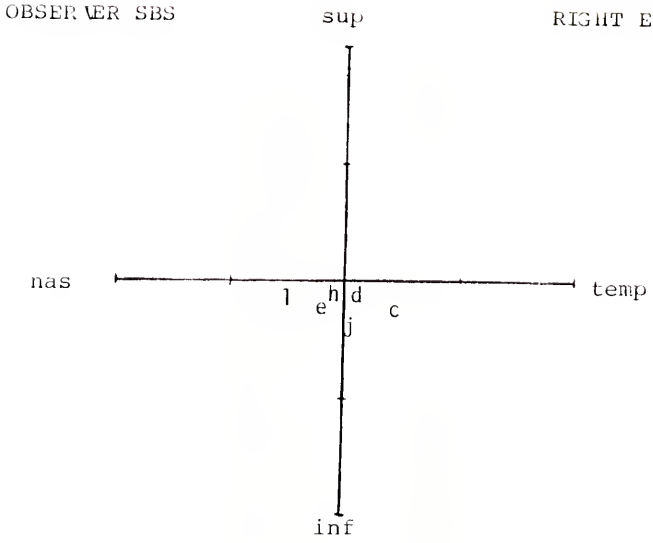
p 15° IVF

(C) Control Eye

(D) Nonamblyopic Eye of Amblyopic Observer

(A) Amblyopic Eye of Amblyopic Observer

Hash Marks Define 2 mm Intervals in Entrance Pupil


OBSERVER SBS
sup
RIGHT EYE (C)
nas
temp
l
e
h
d
c
j
inf

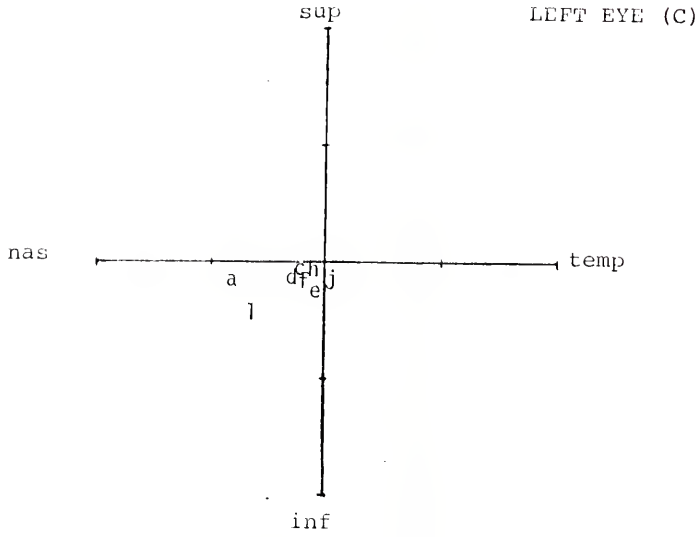

sup
LEFT EYE (C)
nas
temp
a
l
d
e
h
j
inf

FIGURE 4

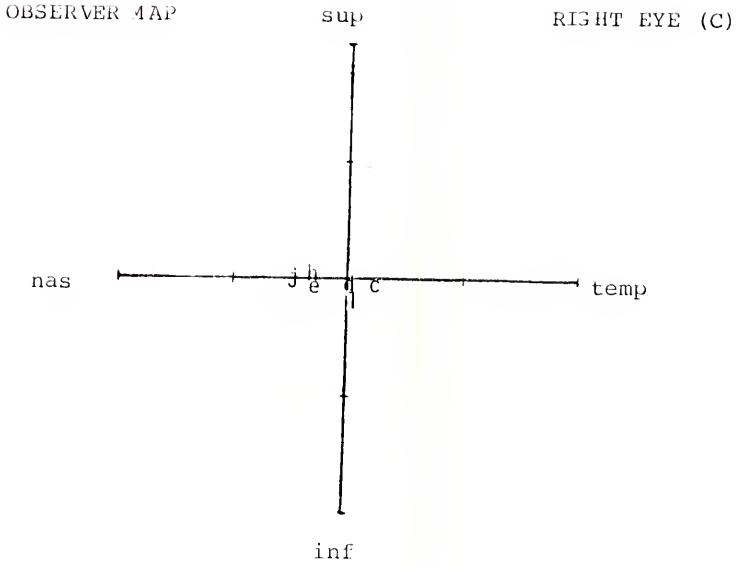

OBSERVER MAP
sup
RIGHT EYE (C)
nas
temp
inf
sup
LEFT EYE (C)
nas
temp
inf

FIGURE 5

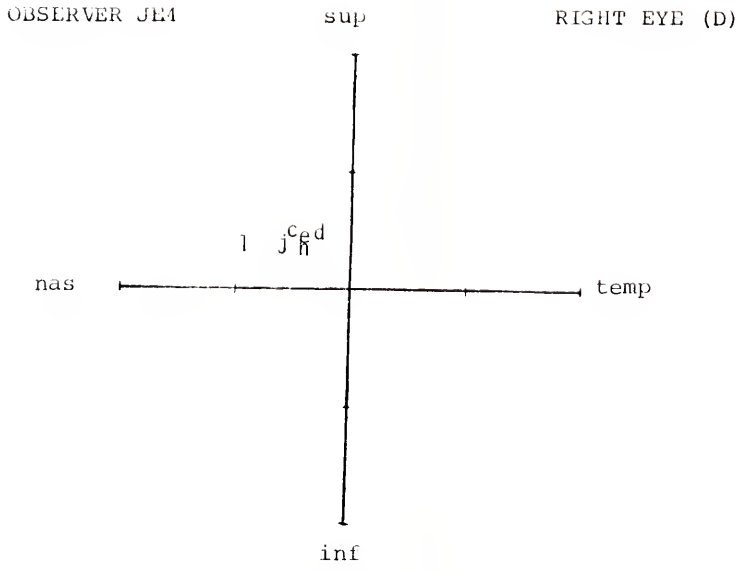
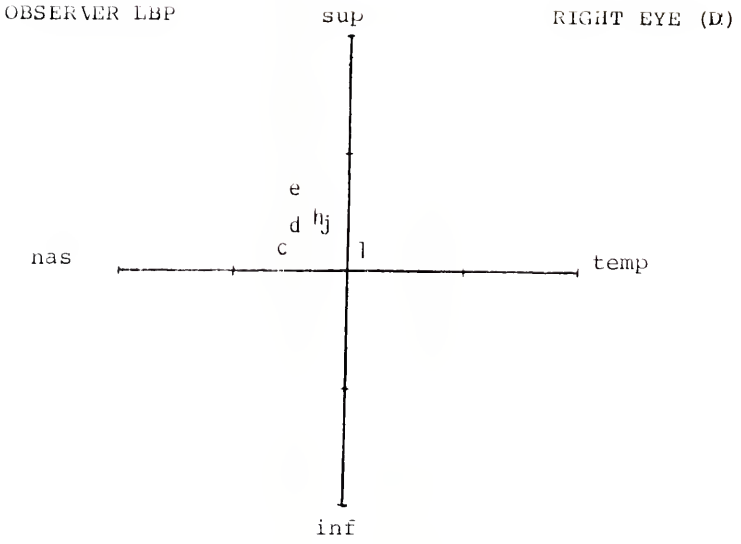

OBSERVER JEM
sup
RIGHT EYE (D)
l
j
c
e
d
h
nas
temp
inf
sup
LEFT EYE (A)
h
f
i
j
l
nas
e
d
temp
inf

FIGURE 6


OBSERVER LBP
sup
RIGHT EYE (D)
e
d
h
j
c
l
nas
temp
inf

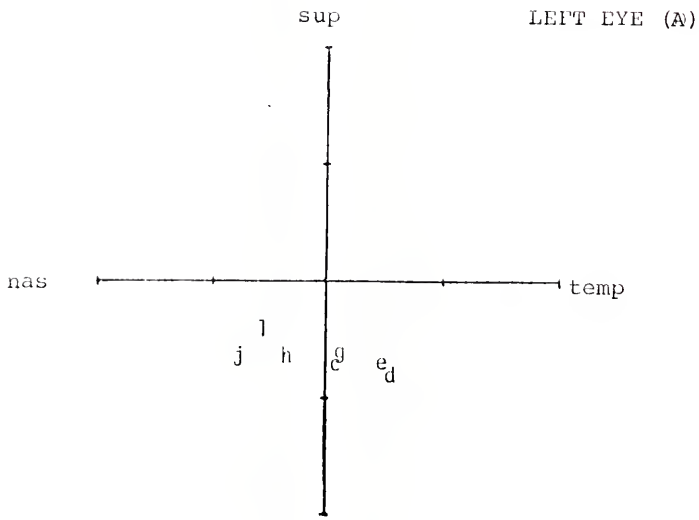
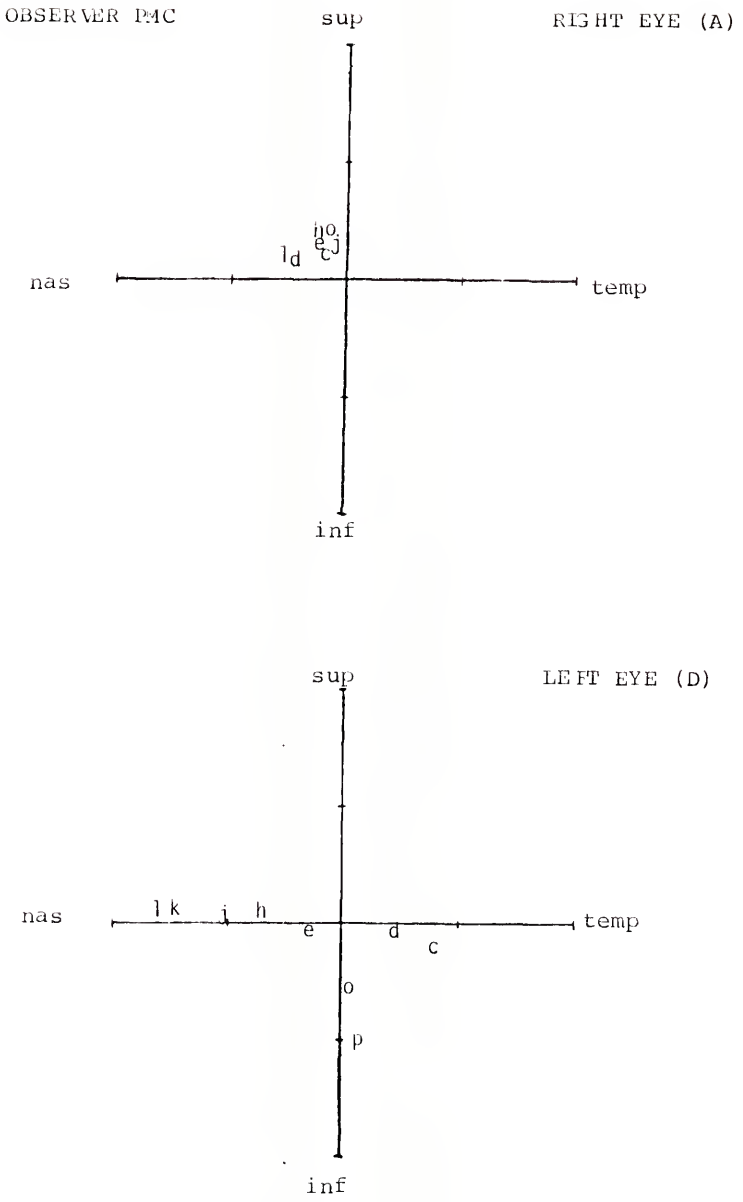

sup
LEFT EYE (A)
nas
temp
l
j
h
g
c
e
d
inf

FIGURE 7


OBSERVER PMC
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RIGHT EYE (A)
nas
temp
inf
sup
LEFT EYE (D)
nas
temp
inf

FIGURE 8

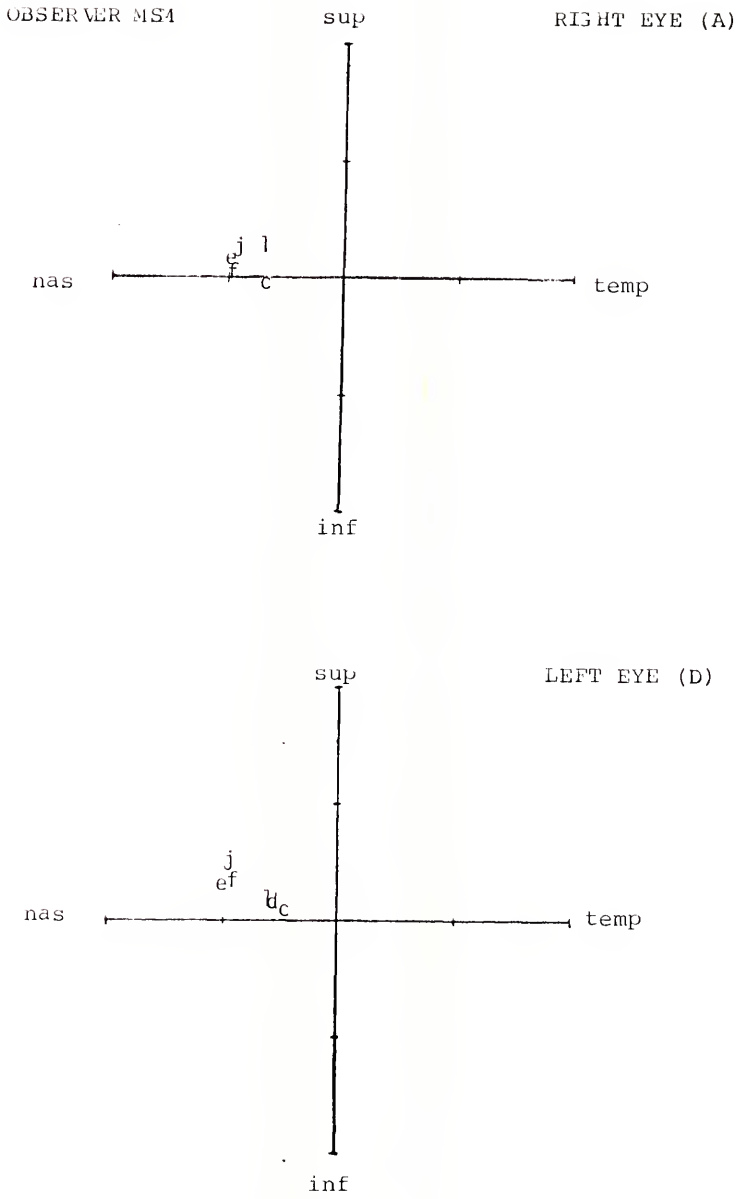
OBSERVER MS4
sup
RIGHT EYE (A)
nas
temp
inf
sup
LEFT EYE (D)
nas
temp
inf

FIGURE 9

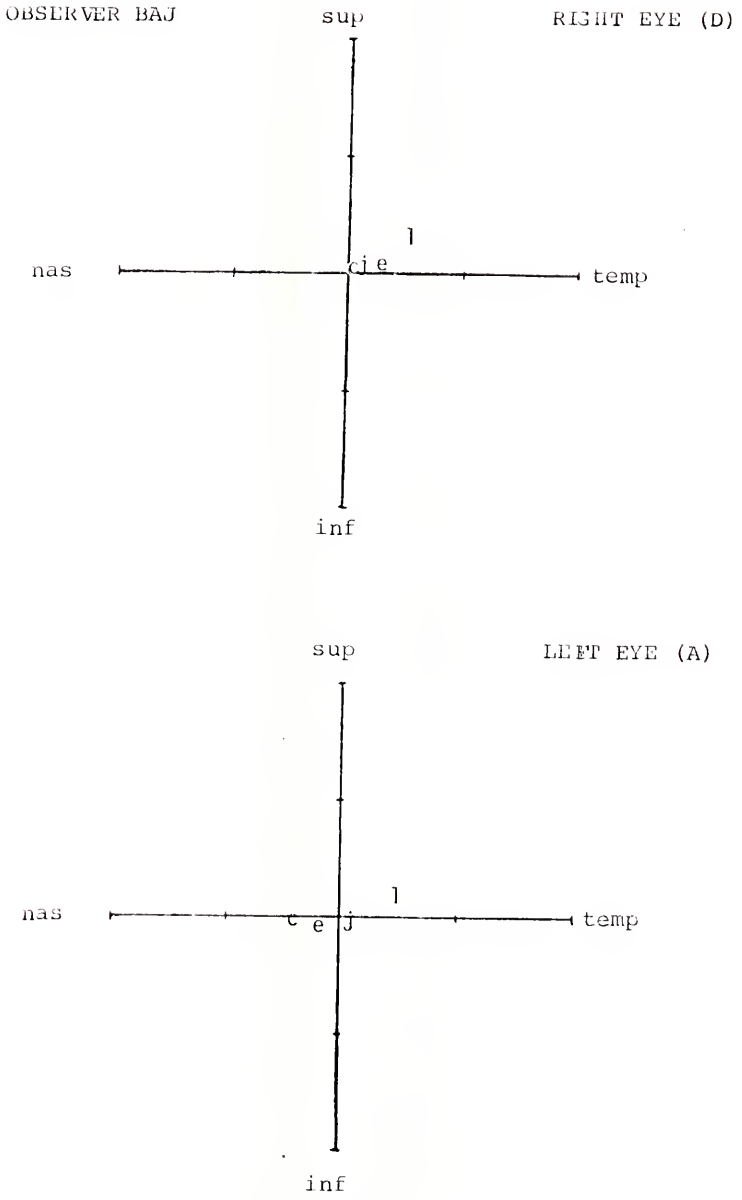
OBSERVER BAJ
sup
RIGHT EYE (D)
l
nas
c j e
temp
inf
sup
LEFT EYE (A)
l
nas
c e j
temp
inf

FIGURE 10

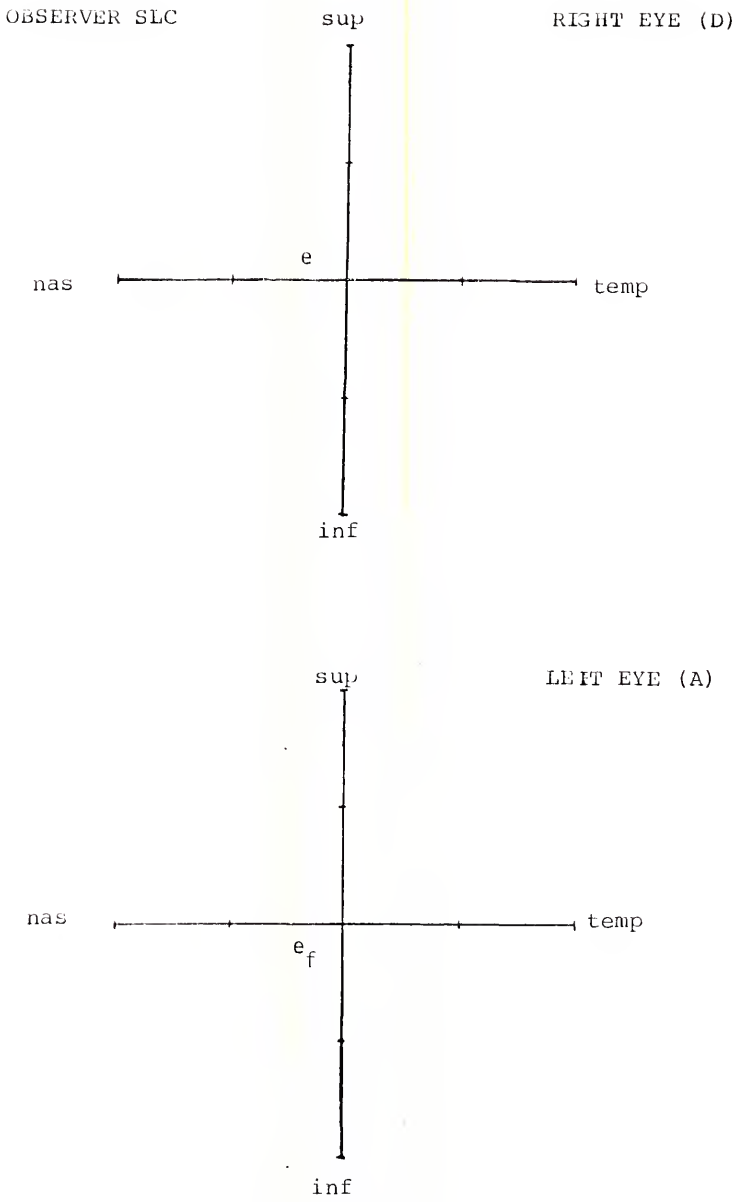
OBSERVER SLC
sup
RIGHT EYE (D)
e
nas
temp
inf
sup
LEFT EYE (A)
nas
temp
e_f
inf

FIGURE 11

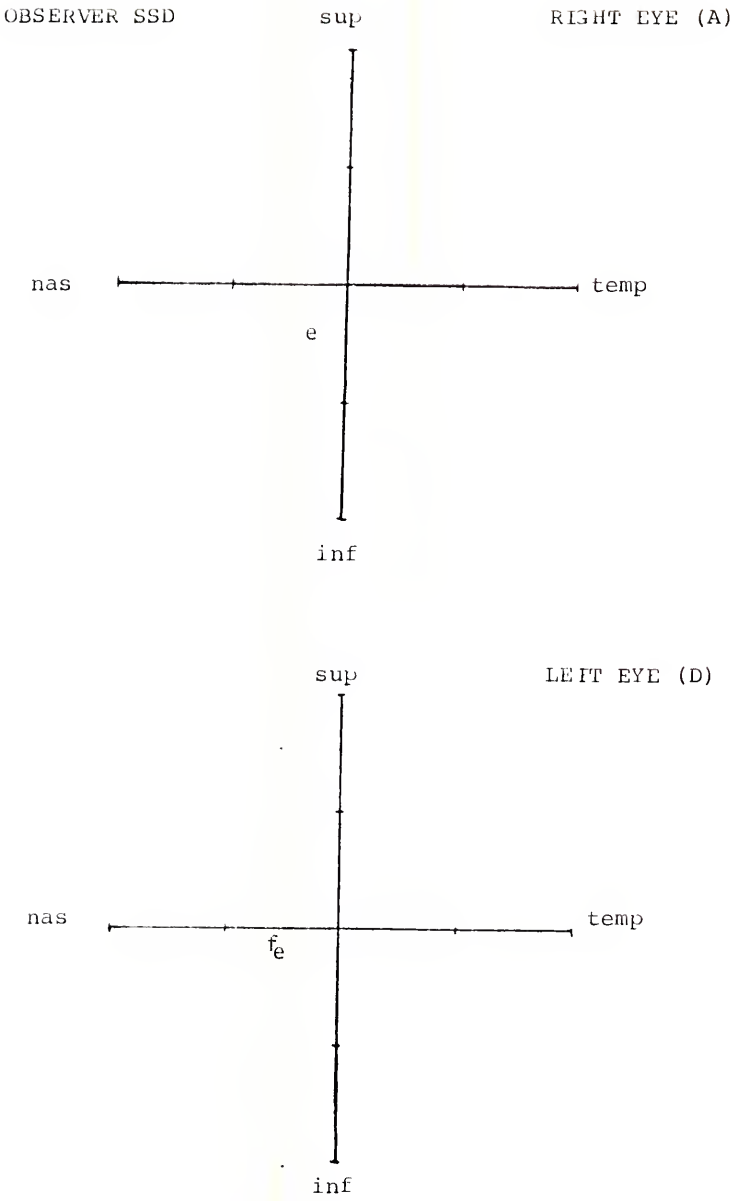
OBSERVER SSD
sup
RIGHT EYE (A)
nas
temp
e
inf
sup
LEFT EYE (D)
nas
temp
f_e
inf

FIGURE 12

These results were unexpected. In fact, the two amblyopic observers SLC and SSD were recruited for SCE function testing at and around the locus of fixation only after no examples of anomalous SCE functions were found in the original sample of 5 amblyopic observers.

In all but one case, the nonamblyopic eyes of the amblyopic observers also revealed estimated SCE function peaks which clustered within a subregion of the dilated pupil. The left, nonamblyopic eye of observer PMC is an obvious exception to this generalization. The results obtained for this eye are considered in detail below.

The estimated SCE function peak locations for both eyes of 5 amblyopic observers tested at a range of visual field positions are shown in Figs. 6 - 10. Estimated SCE function peak locations for SLC and SSD at the locus of fixation and nearby are presented in Figs. 11 and 12. The estimated peak locations for all SCE functions for the individual horizontal and vertical traverses of the pupil, as well as 99 per cent confidence intervals for peaks, are presented for both eyes of all amblyopic observers in Appendix C.

In some cases, the measured amblyopic eye SCE function peaks do not cluster about the pupil center. For example, the SCE function peak locations of observer MSM's right amblyopic eye fall between 1-1/4 and 2 mm from the pupil center (Fig. 9). However, SCE function peak locations determined for the nonamblyopic, fellow eye of this observer are similarly displaced from the pupil center. A tendency

for SCE function peaks to cluster around a region slightly displaced from the pupil center was also observed for one of Enoch and Hope's (1972) normal observers. Displacements of this magnitude are not considered to be indicative of disturbed receptor alignment.

A comparison of the estimated SCE function peak locations within the amblyopic and nonamblyopic eyes of the individual amblyopic observers reveals very little difference in the pattern of estimated peak locations for two of the amblyopic observers, MSM and BAJ (Figs. 9, 10). The clustering tendencies of SCE function peak locations in both eyes of these 2 observers are quite similar to those seen in the control eyes. For observers JEM and LBP (Figs. 6, 7) there is a suggestion that estimated SCE function peak locations within the amblyopic eyes (left eyes of both observers) show a somewhat greater dispersion within the pupil than do the estimated SCE function peak locations of these observers' nonamblyopic eyes, for the range of visual field locations tested. The pattern of estimated SCE function peak locations for observer LBP's left amblyopic eye is indicative of a systematic shift in peak location, in the temporal-nasal pupil meridian, for visual field testing locations between the locus of fixation and 10° NVF. This pattern is seen in Fig. 13, in which SCE functions for horizontal traverses of LBP's left amblyopic eye pupil, for visual field testing locations between 10° TVF and 20° NVF, are presented. Note that SCE function peaks locations for determinations at

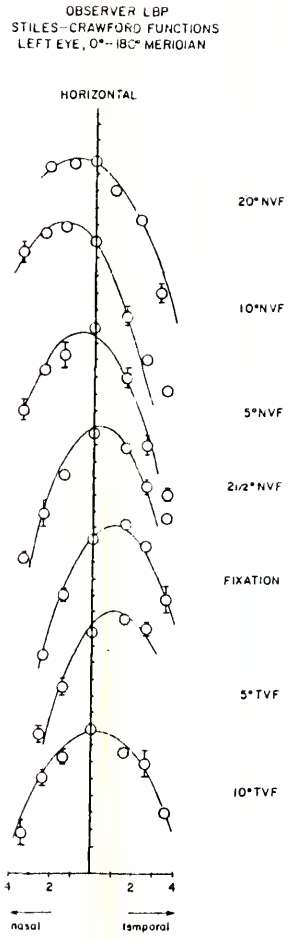

FIGURE 13

Abscissa: Entrance pupil position in mm.
Ordinate: log relative sensitivity hash marks = 0.10 log units.
Curves are vertically displaced arbitrarily.
Error bars = $\pm$ 1 standard error of the mean.

10° TVF and 20° NVF have regressed back toward the pupil center. In fact, none of the estimated SCE function peak locations for the visual field locations tested in this eye deviate far from the center of the pupil.

Thus, within the amblyopic and nonamblyopic eyes of the sample of observers tested, and with the exception of the nonamblyopic eye of observer PMC noted above, retinal receptors apparently tend to align toward a subregion of the exit pupil of the eye. There is a suggestion of an increased dispersion in the locations of the SCE function peaks for the horizontal visual field locations tested in two of the amblyopic eyes. However, the results of the amblyopic observers are not qualitatively different from those obtained for the control eyes.

Within Eye Comparisons of Peak Locations

Despite a remarkable tendency for receptors across a wide region of the retina to apparently maintain alignment toward a restricted region of the exit pupil of the eye, small departures from a common alignment tendency seem to occur within all eyes tested. Thus, within all of the control eyes as well as within all amblyopic and nonamblyopic eyes tested at a range of visual field test locations, two or more of the estimated SCE function peak locations significantly differ in position. This conclusion is based upon a comparison of the boundaries of the confidence intervals defined for the estimated SCE function peak locations at

different visual field test locations (Appendix C). Thus, within each eye tested at a range of visual field locations, 98 per cent confidence rectangles for two or more of the estimated SCE function peak locations fail to overlap. In the absence of observer alignment or other systematic errors, nonoverlapping confidence rectangles indicate that the true SCE function peak locations, and hence inferred receptor alignment tendency, for the two visual field testing locations being compared can be concluded to differ with a confidence of at least 96 per cent.

These significant, albeit small, differences in apparent alignment tendency at different retinal testing locations would seem to be indicative of at least some degree of local retinal control or contribution to receptor alignment tendency. This local contribution might be in the form of regional traction effects upon the retina, for example. The present analysis does not provide insight into the nature of this apparent local component of receptor alignment tendency, however.

Directionality of SCE Functions

The directionality of measured SCE functions was specified using Stiles' (1937) parameter rho (ρ)* and the half

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*For SCE function data fit by the parabola

$$y = b_1 + b_2 + b_3x^2$$

rho is defined by the parameter b_3 (see Chapter VI).

sensitivity half width (Enoch and Bedell, 1978). The half sensitivity half width is defined as the distance within the entrance pupil in mm from the SCE function peak to the location at which luminous efficiency (η) falls to one-half of the value at the function peak. Similarly, when $\log \eta$ is plotted against pupil location, the half sensitivity half width is the distance in the pupil from the peak of the SCE function to the location at which sensitivity decreases by 0.30 log units. Since no special effort was made in this study to empirically locate SCE function peaks or the half sensitivity points precisely, half sensitivity half width values were calculated from the parameters of the parabolas fitted to SCE function data.

Rho values, with 99 per cent confidence intervals, and half sensitivity half widths are tabulated in Appendix D for all observers' SCE function determinations at all visual field testing locations.

Parabolas fit to SCE function data ($\log \eta$ vs. pupil position) typically become flatter (decrease in directionality) as data points further from the SCE function peak are included in the analysis (Stiles, 1937; Safir and Hyams, 1969; Safir et al., 1971; Enoch and Bedell, 1978). Data points beyond approximately 3 mm from the peak often show considerable departure from the parabolas fit to a more restricted range of points (see for example Figs. 13, 15 - 17). Thus, specification of directionality requires (1) precise empirical localization of the SCE function peak and (2) threshold

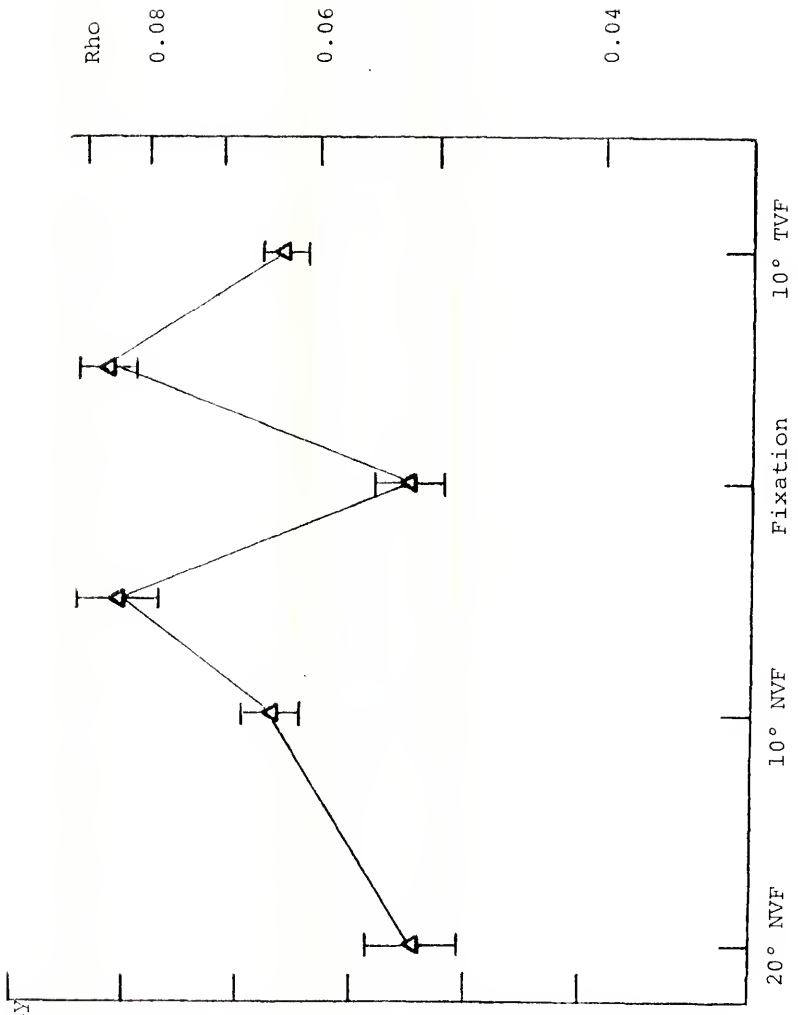
determinations made at pupil locations equally spaced about the peak location at all visual field testing locations. This is essentially the method proposed by Enoch and Bedell (1978) for an empirical specification of SCE function half sensitivity half widths. This study did not employ this strategy and thus directionality estimates may be slightly biased by the locations of the data points with respect to SCE function peaks. However, curve fitting analyses were restricted to data points within 3 mm of the estimated SCE function peak locations.

Despite limitations with regard to specification of SCE function directionalities in this study, the SCE functions determined at different visual field testing locations indicate a clear and orderly change in directionality. Considering the results of the four control eyes, directionality is found to be relatively low (small rho, large half sensitivity half width) at the locus of fixation, increases symmetrically at perifoveal testing locations on both sides of the fixation locus and then declines once again at more peripheral testing locations. These relationships are evident in Fig. 14, which presents the mean of the directionality estimates of horizontal and vertical SCE functions for the four control eyes at each of the visual field testing locations between 10° TVF and 20° NVF.

The increased directionality of SCE functions at perifoveal as compared with foveal testing locations was described by Westheimer (1967) and also by Enoch and Hope (1973). The

FIGURE 14

SCE Function Directionality at Several Visual Field Locations
for Four Control Eyes



Error bars are one standard error of the mean.

latter study indicated that parafoveal directionality values are attained at or before 2° from the fovea. The subsequent fall off at more peripheral testing locations is suggested in Enoch and Hope's (1973) data and is more clearly evident in the results of Bedell and Enoch (1978).

There are individual differences in SCE function directionality as well. Thus, at all test locations other than at fixation, observer SBS shows consistently greater directionality in the SCE functions of both eyes than does observer MAP. However, for both eyes of both observers the same overall trend in directionality for different visual field testing locations is apparent.

The amblyopic eyes and the nonamblycpic eyes of the amblyopic observers tested in this study also show an overall pattern of increasing directionality for perifoveal testing locations and a fall off at more peripheral and at more central retinal locations (Appendix D). There are no clear differences between amblyopic, nonamblyopic and control eyes in this regard.

Westheimer argued that lesser SCE function directionality found at the fovea than at perifoveal testing locations may reflect morphological differences between foveal and extrafoveal cones. Clearly other factors are involved as well since directionality at the fovea and at more peripheral locations is similar despite marked differences in cone shape (Bedell and Enoch, 1978; see above). However, since the SCE function directionality profiles of normal eyes

across foveal and parafoveal locations consistently show smaller directionality values at the fovea, such profiles might be employed to assess whether SCE function testing in the amblyopic eyes of this study was successfully directed within the "morphological" fovea.* Thus, SCE functions determined at the amblyopic eye fovea should reflect a lesser directionality than functions determined at nearby extrafoveal locations. SCE function directionality profiles might thus be used to assess the extent of eccentric fixation. This form of analysis assumes that the foveal regions of the amblyopic eyes examined in this study have undergone no morphological or functional changes which would alter the directionality of SCE functions determined at this location.

On the basis of these considerations, it seems likely that SCE functions determined at the fixation locus for the amblyopic eyes of observers LBP, PMC, and BAJ also included the "morphological" foveal region in these eyes. On the other hand, SCE functions, determined for observer MSM's left amblyopic eye at a test location defined by the location of the entoptically viewed avascular zone of the retinal vessel pattern have a lesser directionality than SCE functions determined at the locus of fixation. Thus, in this

---

*The "Morphological" fovea may be defined as the anatomically specialized foveal region at which relatively low directionality SCE functions are obtained in normal eyes. Based upon Westheimer's argument, it is presumed to be the region in which cone cross sectional dimensions are smallest.

case, SCE function determinations seem to confirm the presence and extent of a monocular eccentric fixation also indicated entoptically. Despite attempts to determine SCE functions at the fovea of observer JEM's amblyopic eye, the directionality values of the obtained functions indicate that such attempts were not entirely successful. However, visual resolution data for this eye (see below) indicate that such attempts must have been near misses. Directionality profiles could not be constructed for amblyopic eyes of observers SLC and SSD since testing was confined to a small region of the visual field in the neighborhood of the fixation locus. Thus, no conclusion as to whether SCE function testing included the foveal region of these observers can be made on this basis.

For one of the control eyes (SBS, left eye) and for two of the nonamblyopic eyes of amblyopic observers (MSM and SSD, left eyes), entoptic projection of the avascular region of the retinal vessel pattern was found not to be centered with respect to the locus of fixation. SCE function determinations at the locus of fixation and at the center of the avascular region of the vessel pattern in these eyes in no instance indicated lesser directionality at the latter testing location. For the first two of these observers, visual resolution measurements were determined at the locus of fixation and at the center of the avascular zone of the vessel pattern as well (see below). These results provide further information concerning the locus of fixation with respect to the fovea in these eyes.

SCE Function Measurements for Observer PMC

SCE Function Peak Locations

SCE functions determined for the left nonamblyopic eye of observer PMC revealed that a systematic change occurred in the locations of the estimated SCE function peaks from approximately 1-1/2 mm temporal of pupil center to the nasal edge of the dilated pupil, for test locations between 10° TVF and 20° NVF in the horizontal meridian of the visual field. Very little vertical change in the estimated positions of the peaks within the pupil was observed over the same range of testing locations. Equal steps across the horizontal meridian of the visual field resulted in approximately equal horizontal displacements of the SCE function peak. Subsequent testing at 25° in the temporal visual field confirmed that this trend continued at a visual field location beyond the position of the blind spot.

The right, amblyopic eye of observer PMC reveals no such trend in SCE function peak locations for test positions between 10° TVF and 20° NVF. Rather, all estimated SCE function peaks for this eye cluster about a region approximately 1/2 mm nasal and 1/2 mm superior to the pupil center. SCE function curves for test locations along the horizontal meridian are shown for observer PMC's left eye in Fig. 15 and for the right eye in Fig. 16.

SCE functions were determined at 10° and 15° in the inferior visual field of PMC's left eye in order to ascertain

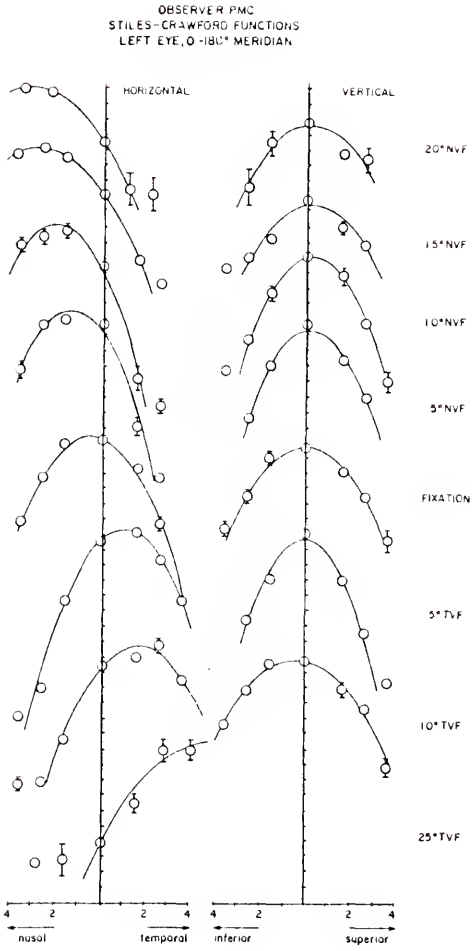


FIGURE 15

For Legend see Fig. 13

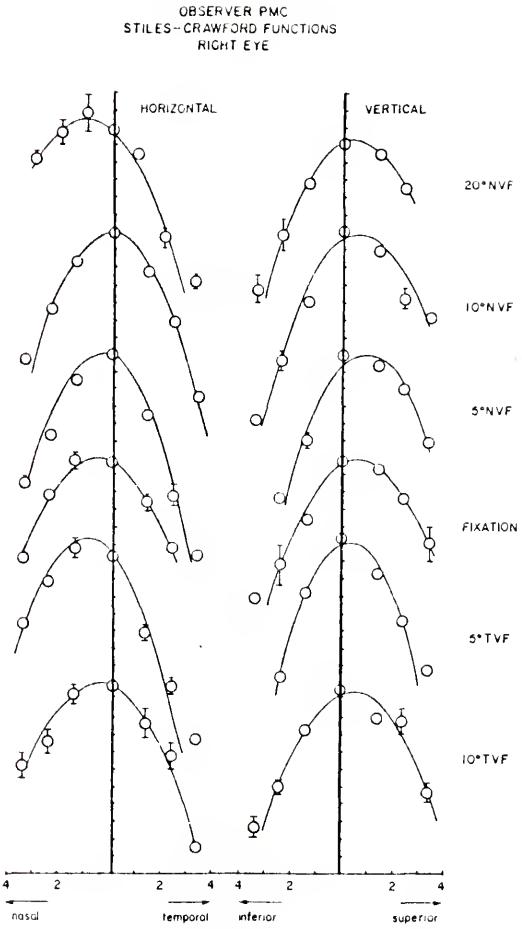


FIGURE 16

For Legend see Fig. 13

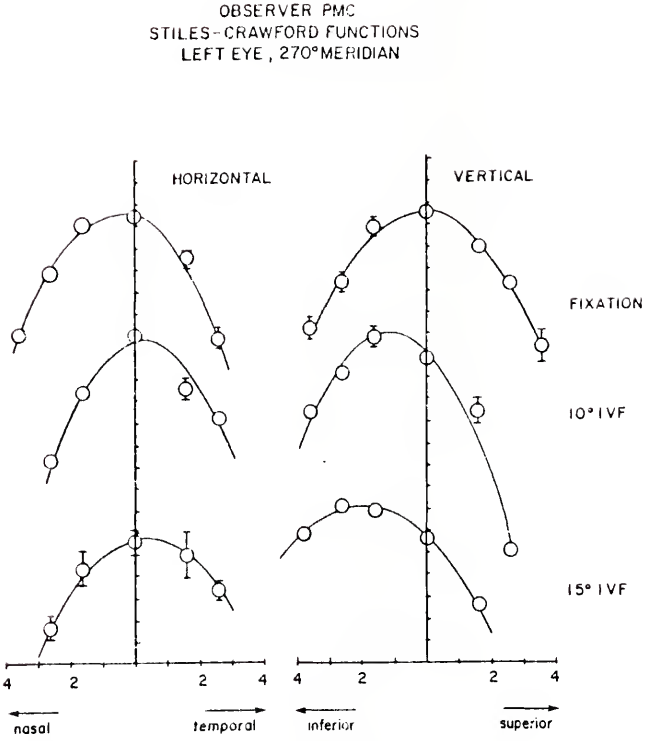


FIGURE 17

For Legend see Fig. 13

whether the systematic changes in estimated SCE function peak locations demonstrated for the horizontal meridian of the visual field could be extended to the vertical meridian. The estimated locations of the SCE function peaks shift approximately from the temporal-nasal axis of the pupil at fixation to 2 mm inferior to the pupil center at 15° in the inferior field. There is a much smaller change in the horizontal positions of the estimated SCE function peaks along this vertical visual field test meridian. SCE functions for PMC's left eye obtained at the fixation locus and at 10° and 15° in the inferior field are shown in Fig. 17.

An SCE function determined at 10° in the inferior visual field for PMC's right eye was found to have its estimated peak position within the cluster of SCE function peak locations found for testing along the horizontal meridian of the visual field (Fig. 8).

The results for PMC's right amblyopic eye indicate that, for the visual field locations tested, retinal receptors tend to align toward a region near the center of the exit pupil. On the other hand, the SCE functions obtained for PMC's left eye across 45° of the horizontal visual field and 15° of the vertical visual field conform to another pattern. The receptors in this eye apparently tend to align more nearly toward the center of the retinal sphere than toward the exit pupil.

This conclusion may be examined using an analysis developed by Enoch and Laties (1971). Enoch and Laties

determined the predicted SCE function peak locations for a range of visual field test locations and for three alternative hypothetical patterns of receptor alignment: (1) alignment toward the center of the exit pupil, (2) alignment toward the center of the retinal sphere, and (3) alignment parallel to a reference receptor at the posterior pole. They assumed that the SCE function peak adequately indicates receptor orientation tendency within the test region and that receptors at the posterior pole of the eye, corresponding approximately to 5° TVF, align directly along the optic axis of the eye, which was assumed to pass through the pole location. Calculations were based upon small angle assumptions, which provide reasonable estimates within about 20°, and the Gullstrand schematic eye modified to be emmetropic.

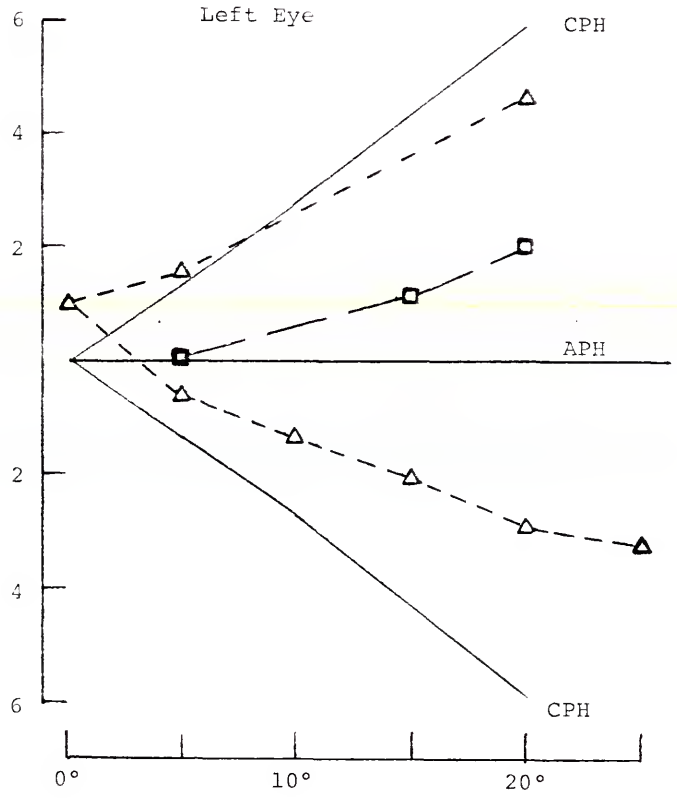
The predictions for idealized retinal receptor alignment toward the pupil center and toward the center of the retinal sphere are shown in Fig. 18. Also shown are the estimated temporal-nasal components of the SCE function peak locations for test locations along the horizontal meridian of the visual field for both eyes of observer PMC. The superior-inferior components of the estimated SCE function peak locations for testing of PMC's left eye within the inferior visual field are also plotted.

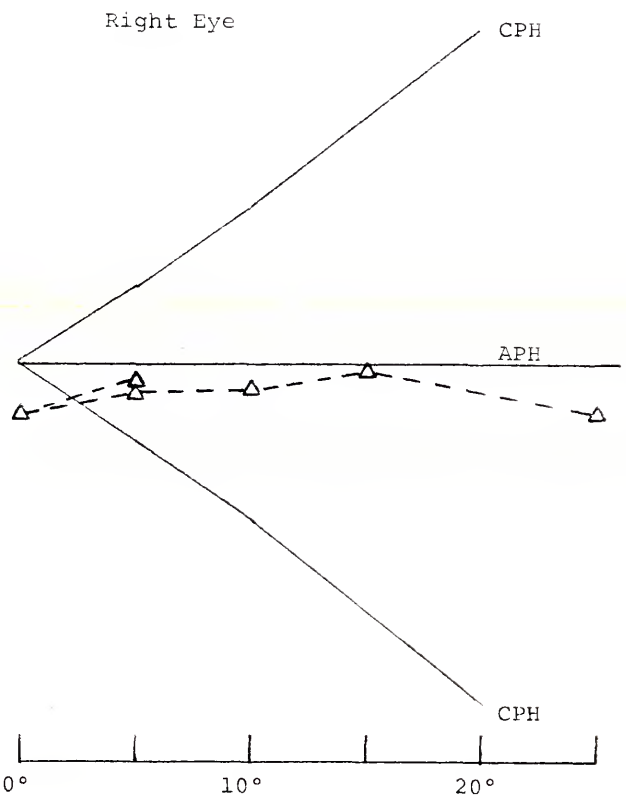
The plotted values for the right, amblyopic eye closely approximate a line parallel to the predictor curve for center of the pupil alignment of receptors. The left eye data more closely conform to the center of the retinal sphere

FIGURE 18

Relationship Between Estimated SCE Function Peak Locations
for Observer PMC and Retinal Receptor Orientation Predictor Curves

Predictor curves for the location of SCE function peaks within the entrance pupil assuming receptor alignment to the center of the exit pupil (APH) or toward the center of the retinal sphere (CPH). Predictor curves are slightly modified from Enoch and Laties (1971). Observer PMC's estimated SCE function peak positions are plotted for horizontal (triangles) and vertical (squares) visual field test locations. Visual field test location relative to the posterior pole (assumed 5° TVF) is plotted on abscissa. SCE function peak location within the entrance pupil in mm is the ordinate.


Left Eye
CPH
APH
CPH
6
4
2
2
4
6
0°
10°
20°


Right Eye
CPH
APH
CPH
0°
10°
20°

alignment prediction. It should be kept in mind that differences between the physical constants of the Gullstrand eye and PMC's left eye may alter the slope of the latter predictor function. In addition, the estimated SCE function peak locations for functions which are displaced toward the margin of the pupil are not considered to be highly reliable, since peak location must be estimated from data points lying on only one side of the peak. However, for at least the retinal region corresponding to the visual field locations tested, receptors within PMC's left eye are concluded to tend to align toward the center of the retinal sphere. The receptors within this observer's right amblyopic eye apparently tend to align toward a region near the exit pupil center.

SCE Function Directionality

A comparison of the directionalities of SCE functions determined at the various visual field testing locations for PMC's left and right eyes is of interest with regard to the different presumed receptor alignment mechanisms operating within the two eyes. Analysis was restricted to SCE functions determined at 10° or less from the locus of fixation in each eye, since the peaks of SCE functions for PMC's left eye at more peripheral testing locations approached the edge of the pupil. The parameters of the fitted parabolas are not considered to be highly reliable for such displaced SCE function peak locations (see above).

In an analysis of SCE function directionalities for test locations within 10° of the fixation locus in the nasal, temporal and inferior visual fields, 12 between eye comparisons could be made. The SCE functions determined for the left eye showed lesser directionalities in all 12 of these comparisons. This result is significant at $p < 0.001$ using the Sign test (Siegel, 1956). While highly statistically significant, the magnitudes of the differences are, in general, not large (see Appendix D). The functional significance of this result is unclear.

Other Measurements Obtained on Observer PMC

One of the aims of this dissertation research was to identify and characterize eyes having anomalous patterns of retinal receptor alignment. It is hoped that subsequent studies of such eyes will yield information as to the nature of normal receptor alignment mechanisms.

The SCE function data presented above for the left eye of observer PMC indicates an anomalous form of retinal receptor alignment within this eye. Receptors apparently tend to align toward the center of the retinal sphere. On the other hand, SCE functions determined for this observer's right eye are indicative of receptor alignment toward the exit pupil. Thus, PMC's right eye provides an excellent control for measurements performed on the left eye. Such measurements are directed toward a further characterization and elucidation of the nature of the receptor alignment anomaly within this observer's left eye.

Some preliminary visual psychophysical and electrophysiological results can be reported at this time. As a part of the SCE function determinations performed for this observer, increment thresholds were obtained over a four log unit range of surround field luminance and at a range of visual field test locations. Increment threshold data for the two eyes and for the different visual field test locations were collected in multiple sessions over a four month period. Despite possible changes in sensitivity or criterion during this period, these data provide an indication of the visual sensitivity contours of the two eyes for test locations between 10° TVF and 20° NVF and at four different adaptation levels. These data are presented in Figs. 19 and 20 as a series of static perimetric plots for the left and right eyes. From the upper to the lower contours, surround field intensity decreases in one log unit steps from a maximum value of 3.54 log photopic trolands (3470 trolands).

Notable aspects of these data are the fairly comparable visual sensitivities at central visual field testing locations, and the poorer sensitivity of the left eye at the 20° NVF testing location. This deficit at 20° NVF appears to be somewhat greater in magnitude for lower as compared with the higher surround field intensities. (None of the surround field intensities at which measurements were made are scotopic.)

Dark adaptometry was performed for visual field test locations 40° in the nasal visual field of the left and

FIGURES 19, 20

Static perimetric sensitivity contours (increasing sensitivity downward) for observer PMC's left (Fig. 19) and right (Fig. 20) eyes. Visual field testing location is the abscissa; log relative threshold for the incremental stimulus is plotted on the ordinate. From bottom to top, curves were determined for one log unit increases in surround field luminance. Surround field luminance for top curve is 3.54 log photopic trolands.

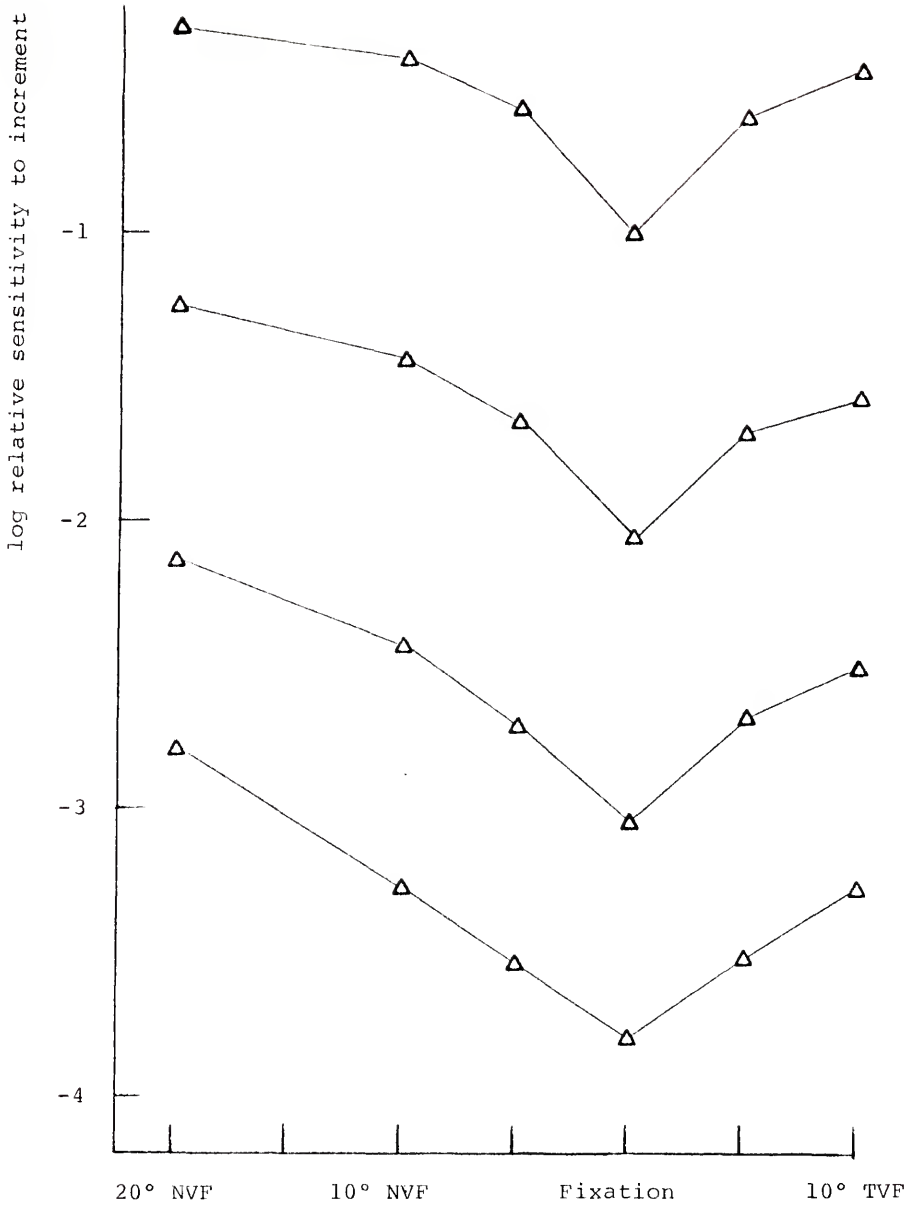


FIGURE 19

Observer PMC, Left Eye

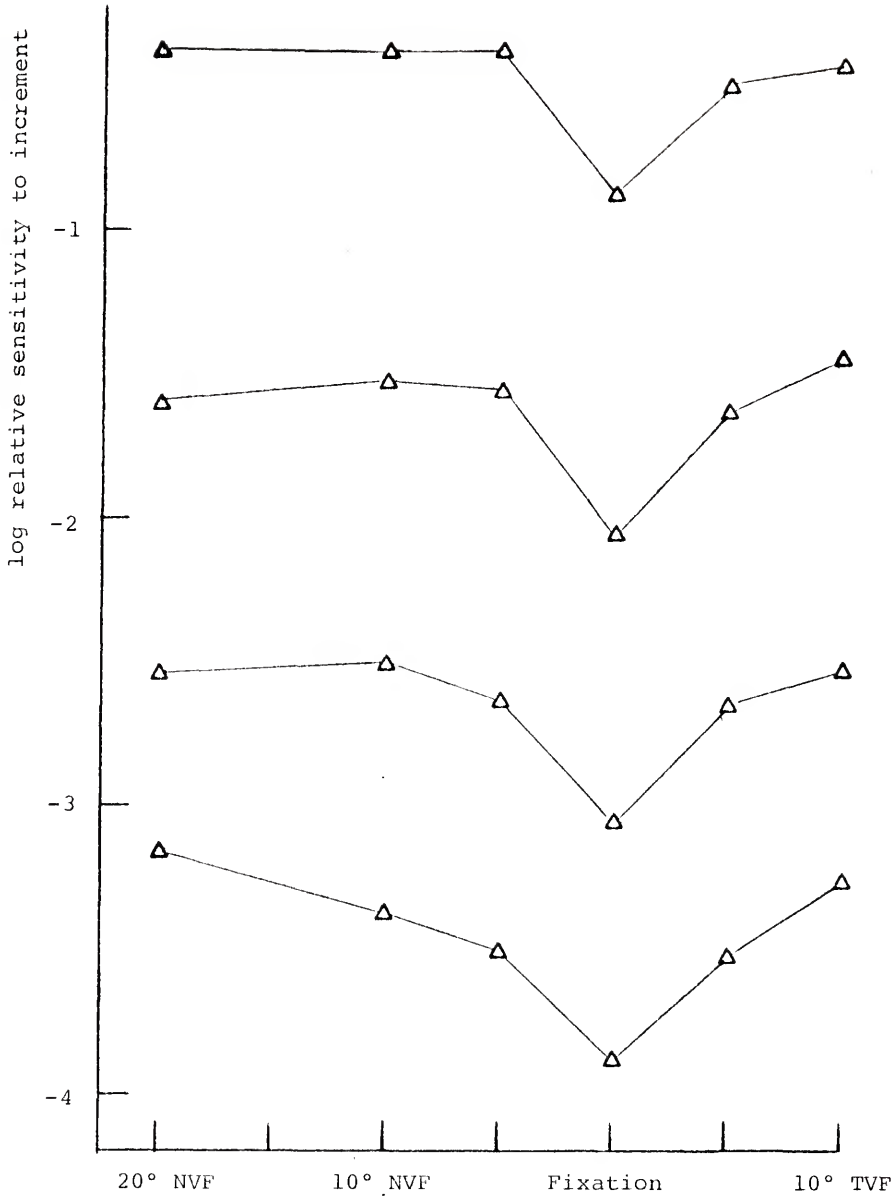


FIGURE 20

Observer PMC, Right Eye

right eyes using a Goldmann-Weekers dark adaptometer (Haag-Streit, Bern) which was available within the Department of Ophthalmology Eye Clinic. SCE functions were not determined at this visual field location for either eye. Preadaptation of 4 minutes to light of 3.38 log cd/m^2 followed 15 minutes of preadaptation in the dark. Left and right eyes were light adapted at the same time and tested in a counterbalanced sequence during the subsequent recovery period (Bedell, 1974). The test stimulus was 12° circular target having a maximum luminance of -0.065 log cd/m^2.

Dark adaptometry results reveal a modest (0.3 log unit) deficit in the sensitivity of the left eye at the time of the cone plateau. Final scotopic thresholds, extended to 45 minutes, do not indicate obvious differences between the sensitivities of the two eyes.

Two electrophysiological procedures were performed for observer PMC using standard clinical procedures at the Department of Ophthalmology Eye Clinic. Electrooculograms (EOGs) were recorded using Ag-AgCl disc electrodes placed at the outer canthus of each eye and referred to a common lead above the bridge of the nose. A ground electrode was placed on the forehead. Potentials were recorded for eye movements of approximately 90° visual angle, as the observer tracked between the positions of two alternately illuminated fixation lights. Signals were AC amplified and fed to a strip chart recorder which provided permanent records of the results. Signals were recorded every 2 minutes during

an 8 minute light adaptation period, during 12 minutes of subsequent dark adaptation, and during 12 minutes of a second light adaptation period. EOGs were calculated for each eye as the ratio of the average amplitudes of the signals taken after 6 minutes in the light and after 12 minutes in the dark.

The light/dark ratios were 213 per cent for the right eye and 230 per cent for the left eye. These values are in the normal range. The magnitudes of the light and dark adapted signals recorded from the two eyes were in approximately the same relationship as these ratios.

Electroretinograms (ERGs) were obtained under light and dark adapted conditions for full field broadband flashed stimuli. Flashes were provided by a Xenon arc source triggered by a Grass stimulator. Signals were recorded using clear corneal contact lens electrodes, placed over the dilated eyes, and fed to separate AC amplifiers for the left and right eyes. Sixteen responses were averaged at each of three light adapted and four dark adapted flash intensities and averaged responses were plotted on a strip chart recorder.

Clear a- and b-waves were seen for both eyes under all light adapted conditions and for the 3 brightest dark adapted conditions. At the dimmest dark adapted flash intensity only the b-wave was seen. Of major interest is that the c-wave appeared to be depressed within the left eye under light adapted conditions. Late differences were also recorded for the dark adapted ERGs, but c-waves of comparable

amplitude were apparent in the records for both eyes. Further analyses of these provocative results are indicated.

Increment threshold data and dark adaptometry indicate a reduced photopic sensitivity within the left eye of PMC at peripheral visual field testing locations. These results are entirely consistent, on a qualitative level, with the SCE function data for this eye. The absence of a noticeable difference in scotopic thresholds between the eyes of observer PMC presumably reflects the lesser directionality of the scotopic retina and/or the inability to detect small differences in threshold with this clinical device.

Both the EOG and the c-wave of the ERG presumably reflect, at least in part, activity of the pigmented epithelim layer (Rodieck, 1973). Anomalies of the c-wave of the ERG seem at this time to be the most promising lead as to the etiology of apparent receptor alignment disturbance within PMC's left eye.

Further studies are planned with this observer. Such studies fall beyond the scope of this dissertation.

SCE Function Results for Observer JEC

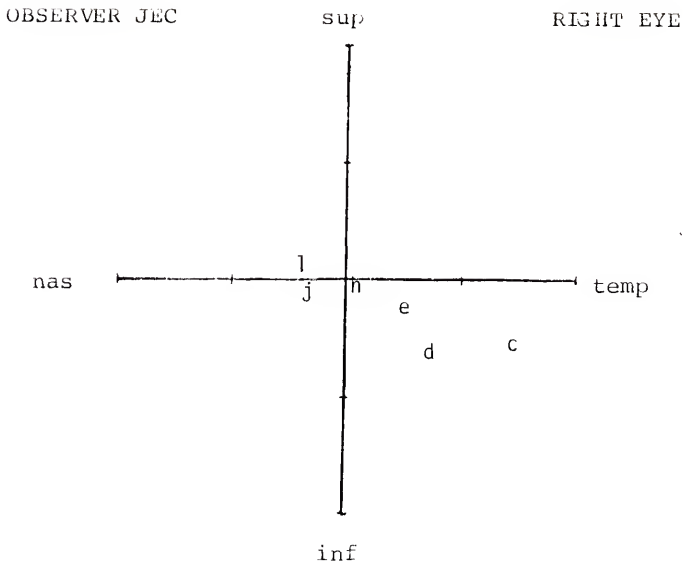
Observer JEC was originally recruited as a control observer. Ophthalmoscopic examination revealed both fundi to have a tesselated pattern of pigmentation. Additionally, possible deteriorative pigmented epithelium changes were seen in the macular region and at the temporal margin of the optic disc in the right eye. Myopic crescents were apparent

in both eyes, that in the right eye being larger. Possible microaneurysms were observed externally on the sclera. The retinal vessels appeared to be within normal limits. This observer has a positive family history of diabetes. In spite of the fundus appearance, visual acuities are 20/15 in both eyes and good stereopsis is achieved (see Appendix B).

Based upon ophthalmosocopic results, observer JEC's data are not presented as control data. SCE function determinations, which were performed in both eyes of this observer, revealed an abnormal pattern of results. The estimated locations of SCE function peaks determined at visual field test locations between 10° TVF and 20° NVF in the right eye and 35° TVF and 20° NVF in the left eye are presented in Fig. 21. The estimated peak locations, as well as 99 per cent confidence intervals, are given for horizontal and vertical traverses of the pupil at all test locations in Appendix C.

For changes in visual field test location from temporal to nasal visual field, estimated SCE function peak locations within both eyes of JEC shift from an inferior and temporal region of the pupil to an area just nasal of pupil center. The temporal visual field testing locations considered correspond to retinal areas between the fovea and the optic disc.

Although there is a trend for estimated SCE function peak locations to shift in a temporal to nasal direction within the pupil for temporal to nasal visual field testing locations, this pattern of results does not seem indicative



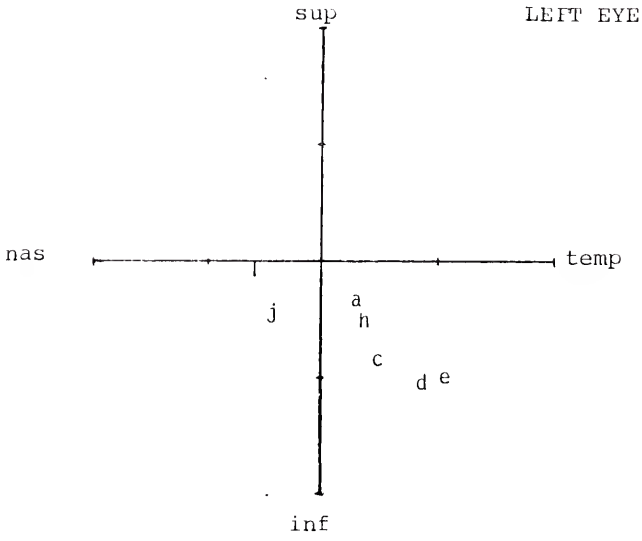


FIGURE 21

Estimated Locations of SCE Function Peaks
at Several Visual Field Testing Locations for Observer JEC
For key see Fig. 4

of center of the retinal sphere receptor pointing. Note that the SCE function peaks in the right eye for all test locations nasal to the fixation locus seem to cluster near the pupil center (Fig. 21). In particular, there is very little nasal shift in the estimated locations of the SCE function peaks between testing locations of 10° and 20° NVF. Also note that within the left eye, a test location at 35° TVF gives estimated SCE function peaks quite near to the pupil center. Thus, the receptor alignment within both eyes of observer JEC seems to be disturbed in the region between the optic disc and the macular region. For at least the right eye, this pattern of SCE function results conforms to the region of ophthalmoscopically revealed anomalies.

Of considerable interest is the location of the estimated SCE function peaks in the two eyes for determinations made at the locus of fixation. Within the right eye, the estimated SCE function peak location is approximately 1 mm temporal and 1/2 mm inferior to the pupil center. In the left eye, the SCE function peak is estimated to be approximately 2 mm temporal and 2 mm inferior to the pupil center, giving a total estimated displacement of about 2-3/4 mm. A markedly temporal and inferior location of the SCE function peak for testing at the fixation locus was consistently found for JEC's left eye over 7 months of data collection. The SCE function for an oblique traverse of the left eye pupil along the axis 150° - 330° (superior nasal pupil to inferior temporal pupil) is shown in Fig. 22. The estimated

FIGURE 22

Left eye function is for a pupil traverse from nasal superior to temporal inferior. For the right eye, horizontal and vertical functions are shown. Abscissa is entrance pupil location in mm; the ordinate is log relative sensitivity. Hash marks on ordinate define 0.5 log unit intervals. Error bars = $\pm$ 1 standard error of the mean.

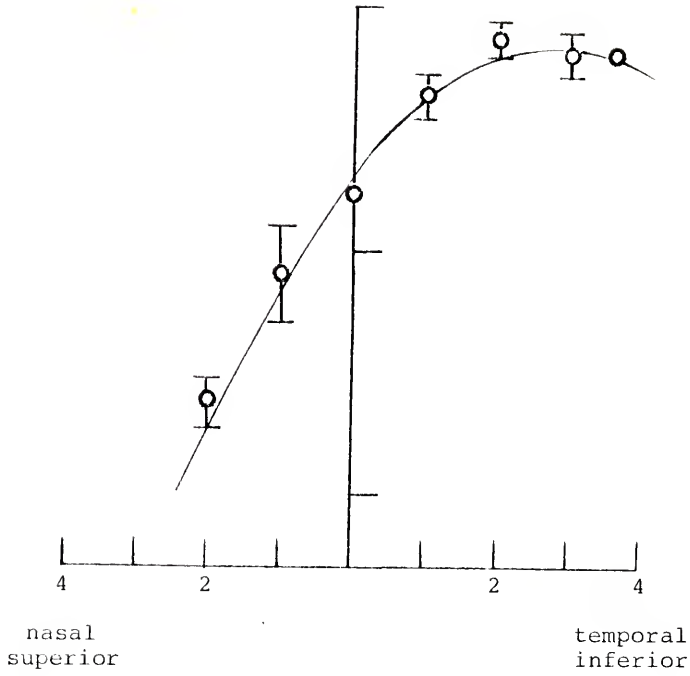
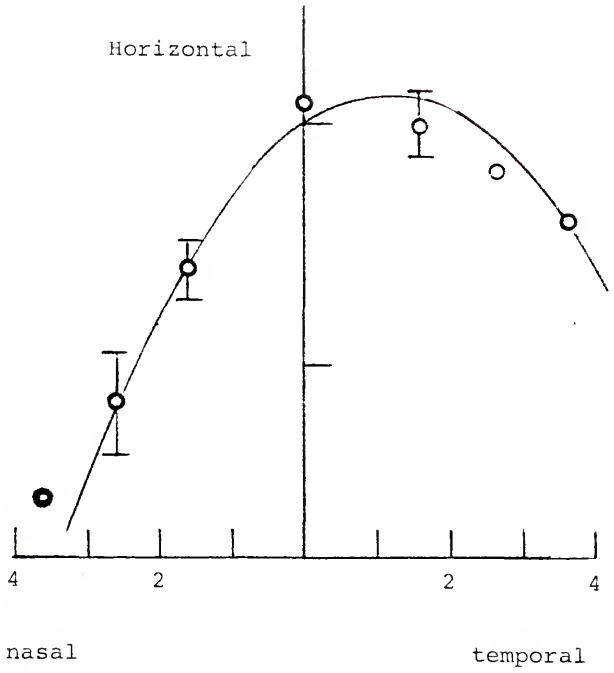


FIGURE 22 A

SCE Function Determined at the Fixation Locus
for Observer JEC's Left (Fig. 22A) and Right (Fig. 22B) Eyes.



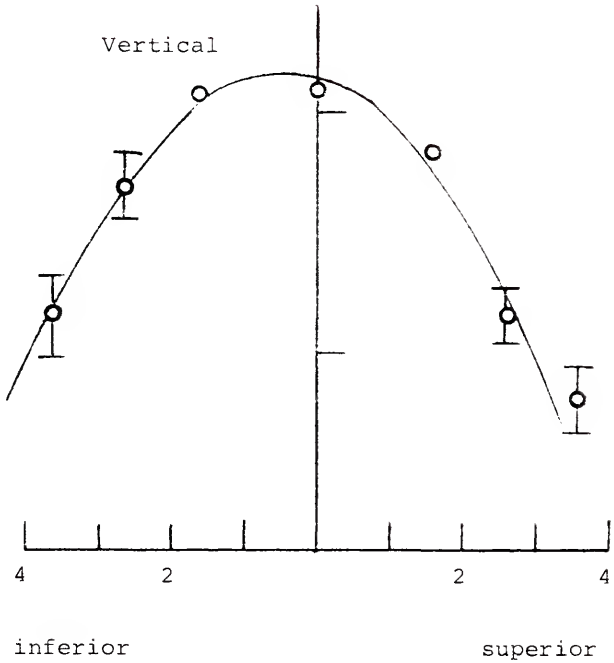


FIGURE 22B

Observer JEC, Right Eye

peak position for this oblique traverse is 2.8 mm displaced from the pupil center (99 per cent confidence interval extends from 2.2 mm from pupil center to beyond the inferior-nasal pupil margin. Also shown in Fig. 22 are SCE functions determined at the locus of fixation for horizontal and vertical traverses of the pupil of JEC's right eye.

The displaced SCE function peak in JEC's left eye and the more nearly centered peak location within the right eye suggested that a comparison of the visual resolution thresholds at the locus of fixation for the two eyes of this observer might give information as to the extent to which a modest amount of presumed photoreceptor tilt affects visual resolution. These data are presented below.

Visual Resolution Thresholds

Control and Amblyopic Observers

The rationale for determining visual resolution thresholds at a number of visual field test locations was to correlate the pattern of visual resolution loss in amblyopic eyes with the pattern of anomalous SCE functions within the same eyes.

The selection of the range of resolution target luminances used in this study (1.16 - 3.16 log photopic trolands) was based upon prior published work using noninterferometrically produced grating targets (Schlaer, 1937). The resolution target luminances used were intended to (1) include the SCE function surround field luminance at the high end and

(2) reveal poorer resolution thresholds for lower target luminances. Since amblyopic eye SCE functions and visual resolution thresholds were to have been compared, the determination of both at comparable luminance levels seemed desirable. Moreover, since visual resolution threshold varies with target luminance (Schlaer, 1937), visual resolution deficits determined at visual field locations at which disturbed SCE functions were also measured might be in some part attributable to an effective decrease in target luminance due to the SCE. By determining resolution thresholds at a range of target luminances, the effect of a decreased effective target luminance, as the result of an anomalous SCE function, could be estimated. Residual resolution deficits due to factors other than a simple decrease in the effective target luminance could then be assessed.

Anomalous SCE functions were not determined at any of the visual field testing locations sampled in any of this group of amblyopic eyes (see above). For this reason, the originally intended form of analysis was obviated. However, aspects of the visual resolution data of the control, amblyopic and nonamblyopic eyes are of interest and are presented here.

The visual resolution data are expressed as the grating half period, in minutes of arc visual angle, at which observers, for a given luminance and visual field condition, were able to discriminate lines up to the right vs. up to the left at a 71 per cent correct threshold. Visual

resolution thresholds measured at different visual field locations do not have equal variances. This is true whether the data are expressed in minutes of arc or as decimal acuities which are reciprocals of minutes of arc.

A Friedman 2-way analysis of variance by ranks was applied to resolution threshold data separately for control, amblyopic and the nonamblyopic eyes of the amblyopes (Siegel, 1956). This analysis revealed that increasing resolution target luminance significantly decreased resolution thresholds only for the control observers at the locus of fixation and for the 0.50° diameter resolution target ($p < 0.01$).

On the basis of this analysis, the resolution thresholds for 1° diameter targets at each of the three luminance levels were treated as multiple estimates of a single resolution threshold at each of the visual field testing locations. The data, collapsed across luminances in this fashion, are presented as resolution thresholds in minutes of arc for the control observers and for observer JEC in Table 1 and for the amblyopic observers in Table 2. Equivalent decimal acuity values are also given in these tables.

The control eye data show that the visual angle subtended by the threshold resolution target, in minutes of arc, increases for increasingly peripheral visual field testing locations. A mean function (resolution threshold contour) for the four control eyes reveals that the increase in minimum resolvable as a function of target location within

Table 1

Visual Resolution Thresholds[#] for 1° Targets as a Function of Visual Field Location for Two Control Observers and Observer JEC

		10° NVF	5° NVF	Fixation	5° TVF	10° TVF
SBS	OD	3.27 ± 0.10 (0.306)	1.91 ± 0.09 (0.523)	0.64 ± 0.04 (1.57)	1.89 ± 0.21 (0.529)	4.37 ± 0.35 (0.229)
	OS	3.36 ± 0.15 (0.298)	1.83 ± 0.18 (0.545)	0.58 ± 0.02 (1.73)	2.07 ± 0.10 (0.484)	4.16 ± 0.22 (0.241)
MAP	OD	3.21 ± 0.30 (0.312)	2.14 ± 0.22 (0.468)	0.60 ± 0.05 (1.67)	1.76 ± 0.07 (0.568)	3.99 ± 0.17 (0.250)
	OS	3.86 ± 0.20 (0.259)	2.25 ± 0.17 (0.444)	0.65 ± 0.06 (1.55)	1.83 ± 0.29 (0.548)	4.12 ± 0.17 (0.243)
JEC	OD	4.48 ± 0.19 (0.223)	2.38 ± 0.20 (0.419)	0.65 ± 0.08 (1.53)	2.17 ± 0.16 (0.461)	4.69 ± 0.49 (0.213)
	OS	4.39 ± 0.66 (0.228)	2.38 ± 0.38 (0.421)	0.77 ± 0.17 (1.30)	2.24 ± 0.37 (0.447)	4.43 ± 0.27 (0.226)

[#]Resolution thresholds ± 1 standard deviation. Equivalent decimal visual acuity values given in parentheses.

Table 2

Visual Resolution Thresholds[#] for 1° Targets as a Function of Visual Field Location for Five Amblyopic Observers

	10° NVF	5° NVF	Fixation	5° TVF	10° TVF
JEM OD(D)	4.55 ± 0.40 (0.220)	2.27 ± 0.42 (0.442)	0.61 ± 0.41 (1.65)	1.96 ± 0.06 (0.509)	4.70 ± 0.39 (0.213)
OS(A)*	3.37 ± 0.63 (0.297)	1.92 ± 0.24 (0.520)	1.10 ± 0.17 (0.907)	1.99 ± 0.21 (0.502)	4.22 ± 0.59 (0.237)
LBP OD(D)	7.55 ± 0.04 (0.132)	3.30 ± 0.34 (0.303)	0.78 ± 0.08 (1.28)	2.68 ± 0.52 (0.373)	6.02 ± 0.88 (0.166)
OS(A)	8.73 ± 0.20 (0.115)	4.95 ± 1.28 (0.202)	1.22 ± 0.03 (0.82)	3.78 ± 0.49 (0.265)	6.42 ± 0.59 (0.156)
PMC OD(A)	4.92 ± 0.27 (0.203)	2.72 ± 0.10 (0.367)	0.74 ± 0.14 (1.35)	2.26 ± 0.07 (0.442)	5.26 ± 0.22 (0.190)
OS(D)	3.94 ± 0.03 (0.254)	2.33 ± 0.20 (0.429)	0.57 ± 0.01 (1.75)	2.43 ± 0.10 (0.411)	4.48 ± 0.61 (0.223)

Table 2 - continued

	10° NVF	5° NVF	Fixation	5° TVF	10° TVF
MSM OD(A)	5.73 ± 1.32 (0.175)	2.84 ± 0.05 (0.352)	0.95 ± 0.08 (1.05)	2.88 ± 0.13 (0.348)	5.68 ± 0.46 (0.176)
OS(D)	4.53 ± 0.45 (0.221)	1.94 ± 0.23 (0.515)	0.70 ± 0.06 (1.43)	2.34 ± 0.56 (0.427)	4.04 ± 0.07 (0.247)
BAJ OD(D)	3.93 ± 0.01 (0.255)	1.75 ± 0.59 (0.573)	0.57 ± 0.00 (1.76)	2.51 ± 0.11 (0.399)	5.34 ± 0.39 (0.187)
OS(A)	4.33 ± 0.47 (0.226)	2.35 ± 0.19 (0.426)	0.57 ± 0.01 (1.76)	2.58 ± 0.25 (0.387)	5.78 ± 0.21 (0.173)

#See note Table 1

*For this observer's amblyopic eye, test locations are specified with respect to the presumed location of the fovea rather than as visual field locations.

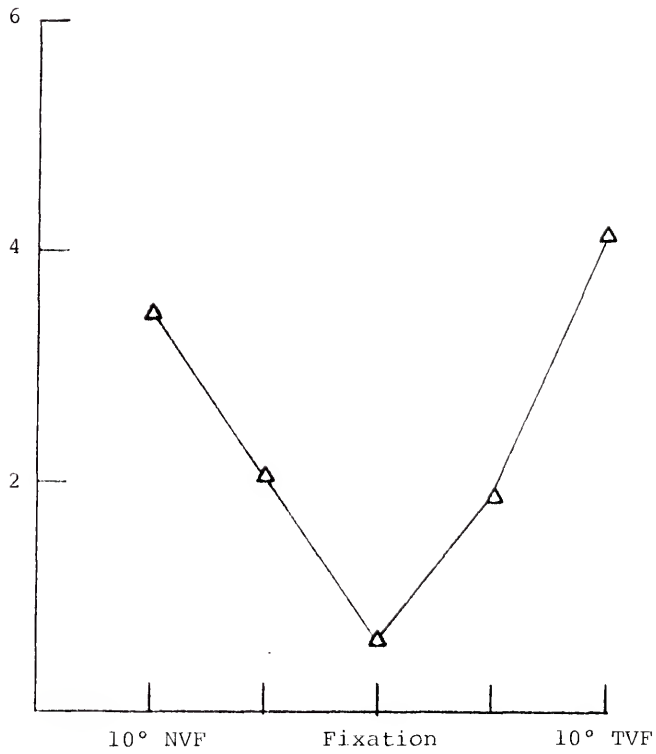


FIGURE 23

Mean Visual Resolution Contour for Four Control Eyes

Visual field testing location on the abscissa, resolution threshold in minutes of arc on the ordinate.

the visual field is essentially symmetrical about the fixation locus (Fig. 23). This is the classical picture of the change in minimum resolvable target dimension with changes in visual field test location (e.g., Mandelbaum and Sloan, 1947).

Resolution threshold contours for the amblyopic and non-amblyopic eyes of this sample of amblyopic observers also reveal resolution minima and clearly increasing resolution thresholds at testing locations on either side of the minimum (Table 2). For the amblyopic eyes of observers LBP, PMC, MSM and BAJ resolution threshold minima for 1° diameter targets are found at the locus of fixation. However, for the amblyopic eye of observer JEM, which was determined to have a monocular eccentric fixation of between 5° - 6°, a resolution threshold minimum was found at the visual field location nearest to the presumed location of the fovea. Much poorer resolution thresholds were measured at the locus of fixation in this eye. (Fig. 24; note that in Table 2 visual field location for this eye only has been corrected for the estimated magnitude of eccentric fixation.) Entoptic tests indicated that observer MSM had a smaller angle of amblyopic eye eccentric fixation (1-1/2° - 2°). Resolution thresholds determined for MSM's amblyopic right eye, using 0.50° diameter targets presented at the locus of fixation and at the center of the entoptically viewed avascular zone of the retinal vessel pattern, also revealed superior resolution thresholds at the presumed locus of the fovea, rather than at the position of eccentric fixation (Table 3).

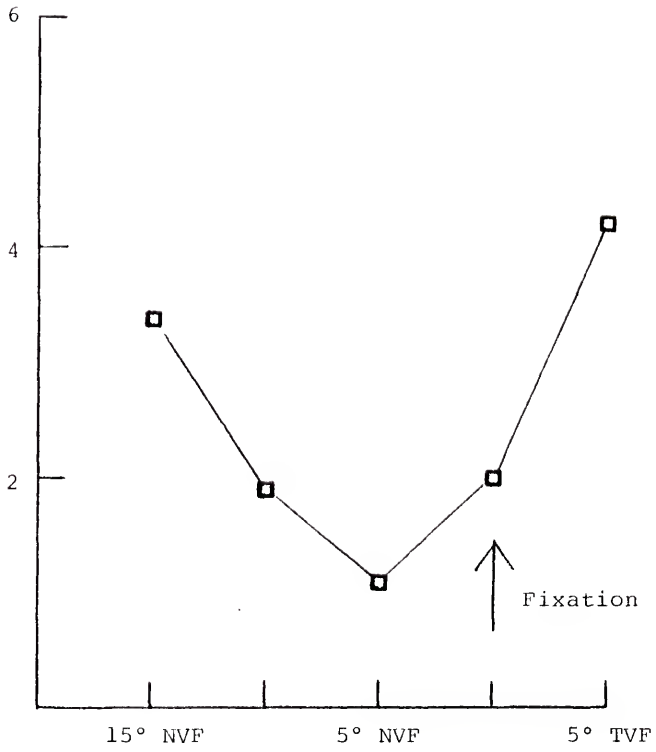


FIGURE 24

Visual Resolution Contour for the Left Amblyopic Eye of Observer JEM

For legend see Fig. 23. Arrow indicates fixation locus.

Table 3

Visual Resolution Thresholds[#] for 0.58° Targets
at the Locus of Fixation and
at the Position of the Entoptic Fovea
for Observer MSM's Right, Amblyopic Eye

Log Relative Target Luminance	Fixation	"Fovea" (1.96° NVF)
-0.5	1.12 ± 0.05 (0.836)	1.01 ± 0.04 (0.987)
-1.5	1.37 ± 0.14 (0.731)	1.05 ± 0.02 (0.955)
-2.5	1.57 ± 0.14 (0.638)	1.21 ± 0.09 (0.83)

[#]See note Table 1.

A comparison of the visual resolution thresholds achieved in these amblyopic eyes for interferometrically formed grating targets with the visual acuities for Landolt targets obtained by the same eyes reveals a marked superiority of the grating target results. The control eyes and the nonamblyopic eyes of the amblyopic observers show similar but less striking differences. Thus, observer JEM, whose amblyopic eye Landolt visual acuity was $20/175^{-1}$, was able to discriminate grating targets presented at 5° in the nasal visual field, near the presumed locus of the fovea, having a half period corresponding to a visual acuity of nearly 20/20 (Table 2, Fig. 24). This observer's Landolt acuity was not improved by eccentric viewing of these targets, in order to compensate for the extent of monocular eccentric fixation. Observer BAJ obtained the minimal possible resolution thresholds within this instrument (0.57 minutes of arc) for 1° diameter grating targets in both eyes. Since these readings are "pinned" on the high side, there is no way to evaluate possible resolution differences between the eyes of this observer for 1° diameter targets. This observer did perform slightly better for 0.50° diameter grating targets with the nonamblyopic right eye than with the amblyopic left eye (right eye, 0.63 ± 0.10 min of arc; left eye, 0.69 ± 0.10 min of arc).

Gstalder and Green (1971) have previously noted that visual acuities determined for amblyopic eyes with interferometrically formed grating targets were often markedly

superior to estimates of visual acuity obtained for the same eyes using more conventional types of targets. Neither luminance nor contrast differences between the two types of targets seem to account for these results. Assuming 3 - 3-1/2 mm pupils, the retinal illuminance provided by the Landolt target chart was comparable to the middle (-1.5 log ND condition) luminance interferometrically formed target. Landolt targets were determined to have slightly higher contrasts than the grating targets (0.80 vs. 0.71). The use of a forced choice psychophysical procedure may have decreased estimated resolution thresholds for the grating targets. However, this is unlikely to be the entire source of the effect. It seems likely that differences in the judgments required for discriminating grating orientation as opposed to specification of the position of detail in the Landolt targets plays a role in this result.*

When the resolution thresholds of the amblyopic and the nonamblyopic eyes of this sample of observers are compared, poorer resolution thresholds at both central and peripheral visual field test locations are seen for 4 of the 5 observers. The exception to this generalization is observer JEM, for whom resolution thresholds are superior at peripheral retinal locations in the amblyopic eye, other

*Viefhues and Kühnhardt (1958) reported that amblyopic resolution was determined to be superior when objective (optokinetic nystagmus) measures as opposed to subjective reports of the presence or absence of grating targets were employed.

than at 5° temporal to the location of eccentric fixation in this eye. Including JEM in the analysis, and pooling across the four noncentral testing locations, (5° and 10° temporal and nasal), nonamblyopic eyes revealed lower resolution thresholds than amblyopic eyes of the same observer in 16 of 20 possible comparisons. This difference is significant at $p < 0.05$ as indicated by the Sign test (Siegel, 1956). If JEM's data are exluded, then in 15 of the 16 remaining comparisons, and for all comparisons at 10°, nonamblyopic eyes have lower resolution thresholds. Differences are on the order of 0.5 - 1.0 minutes of arc. For the purposes of this analysis, both JEM's and MSM's data were corrected for the estimated magnitudes of monocular eccentric fixations.

Except for observer PMC, visual resolution thresholds were determined for the nonamblyopic eyes of the amblyopic observers in the first of two sessions. Thus, the advantage of any practice effect would be given to the amblyopic eyes. Practice effects are often marked for peripheral visual tasks (e.g., Johnson and Leibowitz, 1974).* Moreover, the two alternative forced choice procedure used was designed to eliminate the influence of possible differential criteria which the amblyopic observers might have employed when making judgments with the amblyopic and nonamblyopic eyes.

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*All observers had considerable prior experience with peripheral visual testing, as a result of the SCE function determinations, before initiating visual resolution threshold measurements. Practice effects were therefore expected to be small.

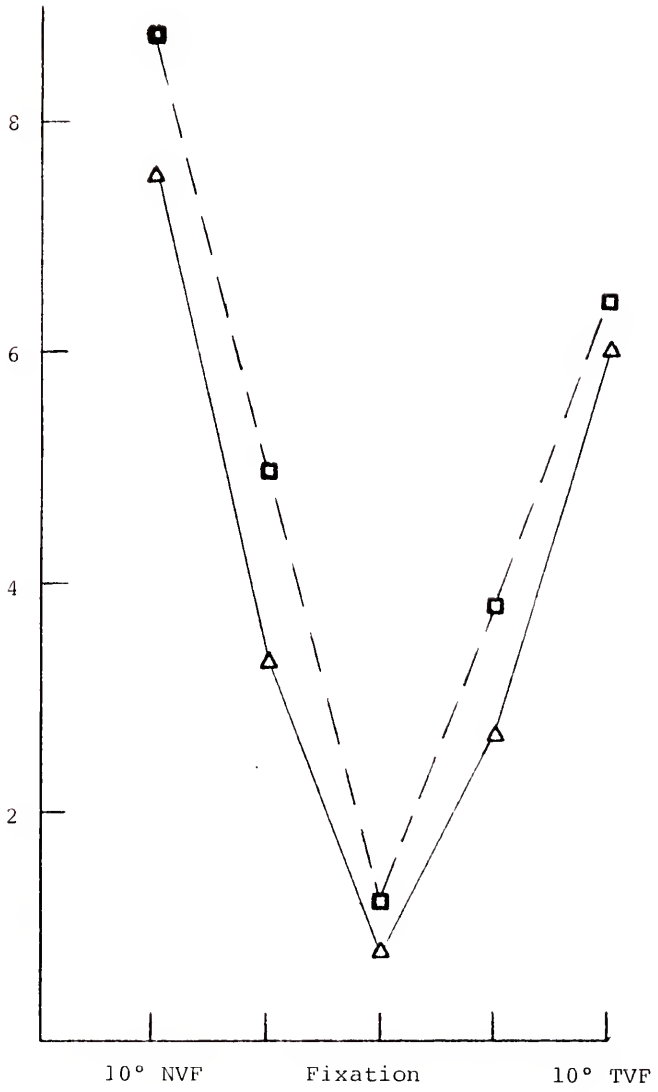

FIGURE 25

Visual Resolution Contours for Both Eyes of Observer LBP

For legend see Fig. 23. Right, nonamblyopic eye: triangles
Left, amblyopic eye: squares

These considerations indicate that this finding seems to reflect real differences in this sample of amblyopic eye and nonamblyopic eye resolution thresholds which extend to at least 10° in the peripheral field for this type of target. An example of between eye resolution differences for one amblyopic observer of this sample is shown in Fig. 25. Observer LBP's right, nonamblyopic and left, amblyopic eye resolution thresholds are presented as a function of visual field testing location. Resolution thresholds of both eyes of this observer are poorer at all visual field testing locations than those of any of the control eyes (compare Tables 1, 2; see Fig. 23).

It is of interest that had visual resolution thresholds been expressed as decimal acuities, rather than in terms of minutes of arc, the between eye differences in resolution target thresholds for the amblyopic observers at peripheral visual field locations would have been rendered very slight (see Table 2). That is, the apparent differences in the visual resolution thresholds of amblyopic and nonamblyopic eyes found at peripheral visual field testing locations might have been obscured by a transformation of the data to decimal visual acuity values.

Resolution Thresholds for Observer JEC

Observer JEC was found to have a markedly displaced SCE function peak at the locus of fixation in the left eye and a more nearly centered SCE function peak for this test

location in the right eye (Fig. 22). The pattern of SCE function peak locations within both eyes of this observer for a range of visual field test locations along the horizontal meridian of the visual field appear anomalous (Fig. 21), especially for testing locations between the fovea and the optic disc. These SCE function data may be related to the appearance of the fundi, which is atypical in both eyes (see above, also Appendix B).

Despite the possibility of a subclinical or incipient pathology in these eyes, JEC's SCE function data provided an opportunity to assess the effect of a clearly displaced SCE function, and hence presumably a modest amount of receptor tilt, upon visual resolution capacity. Using O'Brien's (1946) value of 2.5° per mm in the entrance pupil, receptors at the locus of fixation in JEC's left eye are estimated to be tilted 7° - 8° from an axis joining the pupil center and the fixation locus. Entoptic tests indicate that fixation is centered within the fovea for both eyes of this observer.

Visual thresholds for the left and right eyes of observer JEC for 1° and 0.50° diameter targets presented at the locus of fixation, as a function of target luminance, are presented in Table 4. Much of these data were collected with the right and left eyes tested in a counterbalanced sequence during the same session. For both of these target sizes, left eye resolution thresholds are inferior at the lower (-2.5, -3.5) target luminances. Little difference between the eyes is evident at the two higher luminance

Table 4

Visual Resolution Thresholds[#] for 0.50° and 1° Targets
Presented at the Locus of Fixation for Observer JEC

Log Relative Target Luminance	1° Target		0.50° Target	
	Left Eye	Right Eye	Left Eye	Right Eye
-0.5	0.59 ± 0.02 (1.69)	0.58 ± 0.02 (1.72)	0.73 ± 0.07 (1.37)	0.74 ± 0.01 (1.35)
-1.5	0.76 ± 0.07 (1.32)	0.66 ± 0.10 (1.52)	0.78 ± 0.09 (1.28)	0.80 ± 0.02 (1.25)
-2.5	0.95 ± 0.02 (1.05)	0.71 ± 0.04 (1.41)	1.05 ± 0.14 (0.95)	0.78 ± 0.05 (1.28)
-3.5	1.26 ± 0.03 (0.79)	1.13 ± 0.03 (0.88)		0.21 ± 0.13 (0.82)

[#]See note Table 1.

conditions. These data indicate that a small amount of presumed receptor tilt is not the resolution limiting factor for high luminance interferometrically formed targets, at least for this observer. A presumed modest amount of receptor tilt does apparently influence resolution thresholds at lower target luminances. The reduction of effective target luminance, due to the displaced SCE function within this observer's left eye, appears to be responsible for at least a part of the observed resolution differences.

The magnitude of the apparent resolution reduction is not dissimilar from that reported by Enoch (1971) for optical studies of excised retinas. Possible differential resolution decrements for grating targets oriented in different directions, i.e., parallel and perpendicular to the direction of presumed receptor tilt, have not been assessed for this observer.

Visual Resolution Thresholds at the Locus of Fixation and at the Position of the Entoptic Fovea

Although entoptic tests are commonly used to locate the foveal region with respect to a fixation target (e.g., this study), there is no a priori reason for assuming that the region of smallest cone cross sectional diameter or of closest cone packing (akin to the "morphological" fovea, as defined above) should correspond precisely with the center of entoptically viewed anatomical structures within the foveal or macular region. Rather, a limited amount of decentration between the "morphological" and entoptic foveal centers might easily be imagined to exist.

For one of the control eyes of this study (SBS, left eye) and one nonamblyopic eye of an amblyopic observer (MSM, left eye), the centers of the entoptic fovea, both the avascular zone of the retinal vessel pattern and the centroid of the Maxwell spot were located eccentrically with respect to the locus of fixation. For observer SBS's left eye, the axis of rotation of the Haidinger brush was also displaced with respect to fixation. Both observers reported that a fixated target appeared at or near the edge of the entoptically viewed fovea in their left eyes.

For observer SBS, all three entoptic patterns were similarly displaced 0.6° - 0.9° within the superior-nasal quadrant of the visual field relative to fixation. Observer MSM located the centroid of the Maxwell spot nearer to a fixation target than the center of the avascular zone of the vessel pattern. The former pattern appeared approximately 0.4° - 0.7° nasal to fixation, whereas the avascular region of the vessel pattern appeared almost 1° nasally.

For both of these observers visual resolution thresholds were determined, using 0.50° diameter targets, at the fixation locus and at the center of the avascular zone of the retinal vessel pattern. For observer SBS, resolution thresholds at the locus of the entoptic fovea were determined at a single luminance. For MSM, resolution thresholds were determined at three target luminances. Determinations at the fixation locus and at the center of the avascular region of the retinal vessel pattern were obtained during the same

session in a counterbalanced fashion. For both observers, resolution thresholds were superior at the locus of fixation. For observer SBS, the resolution threshold at the center of the avascular zone was 1.03 ± 0.03 min of arc (decimal acuity = 0.96), and at the locus of fixation was 0.58 ± 0.02 min of arc (decimal acuity = 1.71), for targets presented at -2.5 log relative luminance.

The results for observer MSM's left eye are presented in Table 5. While consistent in direction, the magnitude of the difference between "foveal" and fixational resolution thresholds is smaller than that obtained for SBS. It is possible that within observer MSM's left eye the "morphological" fovea lies between the two locations tested, although presumably nearer to the fixation locus.

These results are in contrast to the resolution data obtained at the locus of fixation and at the entoptic foveal center in two amblyopic eyes (see above). Within the amblyopic eyes, better resolution thresholds were determined at the locus of the entoptic fovea. It should be noted that the extent of decentration of the entoptic fovea with respect to the locus of fixation was larger within the amblyopic eyes than within the control eye and nonamblyopic eye considered here. The center of the entoptic fovea would seem to be a good first approximation to the "morphological" foveal location. From these results it can be concluded, however, that the two do not precisely coincide in all eyes.

Table 5

Visual Resolution Thresholds[#] for 0.50° Targets
at the Locus of Fixation and
at the Position of the Entoptic Fovea
for Observer MSM's Left, Nonamblyopic Eye

Log Relative Target Luminance	Fixation	"Fovea" (1° NVF)
-0.5	0.66 ± 0.04 (1.53)	0.78 ± 0.02 (1.29)
-1.5	0.80 ± 0.02 (1.25)	0.90 ± 0.03 (1.11)
-2.5	0.87 ± 0.01 (1.15)	0.07 ± 0.05 (0.932)

[#] See note Table 1.

CHAPTER VIII
DISCUSSION

Patterns of Inferred Retinal Receptor Alignment

Stiles-Crawford effect (SCE) functions were determined across 30° of the horizontal meridian of the visual field for both eyes of two control observers and for both the amblyopic and nonamblyopic eyes of a sample of five amblyopic observers.

For all of the control eyes and for all but one (nonamblyopic) eye of the amblyopic observers, retinal receptor orientation, as inferred from these SCE function determinations, tended to be directed toward a subregion of the exit pupil of the eye for all testing locations (Figs. 4 - 10). The single exception to this generalization is the left nonamblyopic eye of observer PMC, which is considered in detail below. In this eye receptor orientation apparently follows a different law. The locations of the estimated SCE function peaks for the visual field locations tested indicate that receptors within observer PMC's left eye tend to more closely align toward the center of the retinal sphere (Figs. 8, 15, 17, 18).

SCE function peak locations were determined for another observer over approximately the same range of visual field

testing locations. This observer showed apparent fundus anomalies within both eyes upon ophthalmoscopic examination. An anomalous pattern of estimated SCE function peak locations was found within both eyes of this observer as well. Despite a marked dispersion in the locations of the estimated SCE function peak locations within this observer's eyes, all peaks, including that for a test location at 35° in the temporal visual field of the left eye, remained inside the boundary of the dilated pupil (Fig. 21). Thus, even though an anomalous pattern of receptor alignment at different retinal locations can be inferred for this observer's eyes, a general alignment toward the eye pupil is still apparently maintained at all sampled test locations.

These results confirm earlier work by Enoch and Hope (1972a, 1973) and Bedell and Enoch (1978), who also found evidence of a receptor alignment tendency toward the exit pupil of the eye, across a range of visual field testing locations, using the SCE function as an indicator. The present results also extend those of the earlier studies. In the present case, between eye comparisons of estimated SCE function peak positions can be made for several observers. For the two control observers and for at least two of the amblyopic observers, the patterns of estimated SCE function peak locations within the two eyes appear to be highly similar (Figs. 4, 5, 8 - 10). For two other of the amblyopic observers, the data suggest a somewhat greater dispersion in the locations of the estimated SCE function peak locations

within the amblyopic eyes for the visual field locations sampled (Figs. 6, 7). The suggested differences between the eyes of these latter two observers are not qualitative in nature, but rather seem to be differences in the degree of SCE function peak dispersion within the pupils of the two eyes.

The tendency for receptors at widely separated retinal locations to align toward a subregion of the pupil, as indicated by the clustering of SCE function estimated peak locations within the pupil, suggests that some retina-wide mechanism maintains receptor alignment toward the exit pupil. However, evidence that some local component of receptor alignment exists has been seen in a case in which normal retinal receptor alignment was apparently disturbed by subretinal fluid secondary to trauma (Campos et al., 1978). Subsequently, SCE functions indicative of a recovery of receptor alignment were determined at the originally disturbed foveal region. At the same time, receptors at a nearby parafoveal test location apparently underwent a disruption of alignment. At a later test date, receptors at the extrafoveal test location had seemingly recovered a normal alignment with no further change occurring at the fovea. Entoptic visualization of what are apparently receptor alignment subgroups (see Chapter II) also indicate a local receptor alignment component.

Evidence for a local component of receptor alignment also exists within the present study. Statistically significant differences in estimated SCE function peak location for different testing locations within the same eye were found for all eyes in which SCE functions were determined

across a range of visual field test positions (Appendix C). These differences are on the order of only a few degress in receptor orientation at the retina. A local contribution to receptor alignment is also suggested by the regional systematic shifts in estimated SCE function peak locations found within some eyes (e.g., Figs. 7, 13, 21). For observer JEC (Fig. 21), the pattern of estimated SCE function peak locations within both eyes is indicative of a progressive change of receptor alignment within the retinal region between the fovea and the optic disc. At temporal retinal locations (nasal visual field) alignment more nearly toward the pupil center is apparently maintained. It is hoped that further studies of this observer can elucidate the nature of these presumed local disruptions of alignment.

Inferred Retinal Receptor Alignment in Observer PMC

As a part of this dissertation research, an observer was identified, within one eye of whom the retinal receptors within the range of testing locations sampled apparently align toward the center of the retinal sphere rather than toward the exit pupil of the eye (Figs. 8, 15, 17, 18). Within the fellow eye of this observer, receptors at the same range of testing locations apparently tend to align toward a position near the center of the exit pupil (Figs. 8, 16). Retinal receptor alignment tendency is inferred from the estimated peak locations of SCE functions determined for this observer. Of the many measurements made, none failed to conform to the above patterns.

Prior to this dissertation research, retinal receptor alignment across a range of retinal locations had been assessed psychophysically in fewer than a dozen individual eyes (Aguilar and Plaza, 1954; Enoch and Hope, 1972a, 1973; Bedell and Enoch, 1978). Retinal receptor orientation within the fovea, or at the locus of fixation, has been estimated from SCE functions for many more observers. Note that had SCE function determinations been made for observer PMC only at the locus of fixation, or even at a few degrees on either side of the fixation locus, the apparent tendency of receptors to align toward the center of the left eye would almost certainly have gone undetected. Only measurements across a considerable range of visual field testing locations could have revealed this apparent anomaly. Until further studies of this sort are conducted, there is no way to assess whether the pattern of receptor orientation with PMC's left eye is truly unique nor the frequency of such alignment tendencies among human observers. However, the reported results of carefully performed retinal histological and of X-ray diffraction studies on infrahuman eyes (see Chapter II) have as yet revealed no instance of receptors oriented toward the center of the eye in any of a variety of species.

This observer thus presents a possibly unique opportunity to elucidate the nature of hypothesized retinal receptor alignment mechanisms within human observers. Additionally, the consequences for vision of properly aligned, i.e., directed toward the exit pupil of the eye, receptors may be inferred

from differences in visual functioning between the eyes of this observer. Clearly, such differences are not to be expected at central visual field locations where both pupil pointing and center of the eye pointing patterns of inferred receptor orientation result in receptor alignment appropriately directed toward relevant stimuli entering at the pupil (Figs. 8, 18). The consequences of anomalous retinal receptor orientation of the sort hypothesized for the left eye of observer PMC are to be expected at peripheral visual locations.

Dark adaptation functions determined for a test stimulus at 40° in the nasal visual fields revealed an approximately 0.3 log unit lesser sensitivity (a factor of 2) at the cone plateau in left eye. If any between eye sensitivity difference exists at the final scotopic threshold, it must be quite small and was not detected by the clinical apparatus used. Static perimetric contours (Figs. 19, 20) constructed from increment threshold measurements, reveal a reduction in left eye sensitivity at the most peripheral testing location (20° NVF). Further studies of this sort are indicated, as are SCE function determinations at test locations more peripheral than 25° in the visual field. Scotopic SCE functions determined at peripheral visual field locations would also be of value. Such studies are planned for this observer.

An understanding of the etiology of the apparent receptor alignment anomaly within this observer's left eye would be of tremendous significance. Ophthalmological evaluation

of the fundi reveal no patent abnormalities within either eye or obvious differences between the eyes. Fluoroscein angiography is being considered at this time.

Electrophysiological recordings of electrical events within observer PMC's eyes were hoped to reveal some clue as to the nature of the hypothesized anomaly within the left eye. Electrooculograms (EOGs) indicated no obvious difference in the standing potentials of the two eyes. Additionally, normal light/dark ratios were found in both eyes.

On the other hand, the electroretinographic (ERG) results are highly provocative. Late differences are apparent in the signals recorded from the two eyes, especially as a depressed c-wave in the left eye under light adapted conditions. The c-wave apparently reflects a combination of activity at the pigmented epithelium-retinal receptor boundary (Rodieck, 1973). Anomalies at this location, as suggested by the preliminary ERG results, are certainly situated at a region within the eye at which an anomalous receptor alignment might be reasonably inferred to be a consequence. One might speculate that a component of the electrical activity generated by light within this retional region, which normally has a role in the mechanisms of receptor alignment, is disturbed or absent in PMC's left eye. It is hoped that further electrophysiological studies of this observer will provide additional insight into this question. The fact that this apparent alteration in receptor alignment covers a large part of only one retina suggests a possible developmental or genetic anomaly.

Central and Peripheral SCE Function Directionality

SCE function directionality (rho value or half sensitivity half width) was found to change in systematic fashion from central to peripheral retinal test locations (Fig. 14, Appendix D). This result is in agreement with previous reports (Westheimer, 1967; Enoch and Hope, 1973; Bedell and Enoch, 1978). The reduced SCE function directionality at central retinal locations has been suggested to reflect the morphological specializations of foveal cones, and in particular their small cross sectional diameter. Such an explanation cannot account for the trend of decreased directionality between perifoveal and peripheral retinal testing locations. It is possible that peripheral reductions in SCE function directionality represent, at least in part, the larger retinal receptive field areas at peripheral retinal locations (e.g., Rodieck, 1973). Insofar as psychophysical SCE function measurements represent the summed directionality of groups of small acceptance angle (high directionality) receptors (see Chapter II), then the inclusion of larger numbers of receptors, and hence a greater distribution of individual receptor or receptor group alignment tendencies within single receptive field areas might be expected to broaden the overall directional tendency shown by such receptive fields. Alternatively, one might speculate that at more peripheral retinal locations, SCE functions reveal an increasing rod receptor contribution. Rod directionality is apparently

less than that of cones (e.g., Flamant and Stiles, 1948; vanLoo and Enoch, 1975). Increasing rod contributions seem unlikely because of the rather high luminance levels employed for these determinations (3.04 log photopic trolands) but cannot be ruled out since rod saturating levels might not have been employed.

The Relationship Between Inferred Retinal Receptor Orientation and Amblyopia in the Present Sample of Amblyopic Eyes

The SCE functions measured for this sample of seven amblyopic observers revealed no instance of a clearly anomalous SCE function or displaced SCE function peak. The sample of amblyopic observers tested was recruited from the University campus and Health Center staff populations rather than directly from clinical sources (Chapter V). It is possible that a different sample of amblyopic observers, drawn for example from an Eye Clinic patient population, would have revealed one or more cases in which SCE functions were disturbed. Clinical amblyopia patients suitable for the extensive series of examinations required by this research were not available.

The visual field testing locations at which SCE functions were determined in amblyopic eyes were selected to include both central and near peripheral retinal regions. Every effort was made to measure SCE functions within the foveal region of these amblyopic eyes. A priori considerations indicated that retinal receptor orientation disturbances

within the fovea were most likely to contribute to decreased visual resolution shown by amblyopic eyes. The amount of visual resolution loss which might reasonably be accounted for by receptor alignment anomalies is modest. Thus, it was not deemed likely that possible receptor malorientation at extrafoveal locations, at which visual resolution presumably is limited by retinal receptive field sizes rather than receptor grain mosaic, would meaningfully degrade visual resolution other than by a possible brightness decrement of the resolution target.

Efforts to assess receptor orientation within the foveal region of the amblyopic eyes of this sample met with partial success. Visual resolution contours, SCE function directionality profiles and entoptic projections of the foveal region* were employed to assess whether SCE function determinations were accurately directed within the fovea. It seems likely that in at least four of the sample of amblyopic observers (LBP, PMC, MSM, and BAJ) SCE function determinations were in fact carried out within the foveal region. For three of these observers (all but MSM), foveal testing was apparently accomplished at the locus of fixation. The SCE functions determined at the presumed foveal region in these four amblyopic eyes are not different in any way, other than an expected reduction of directionality, than those obtained at other visual field testing locations

*Subject to the limitations described in Chapter VII.

(Figs. 7 - 10). That is, there is no hint in these data that a selective disruption of receptor orientation occurs at the foveal region of any of the amblyopic eyes of this sample. This conclusion must be limited by the 0.50° diameter of the test target used.

For observer JEM, SCE function determinations were probably not directed precisely to the fovea. This conclusion is based upon the SCE function directionalities at test locations near the presumed location of the fovea, none of which indicate the reduction expected for foveal testing. Several determinations were made at locations near the presumed foveal location for this eye (5° NVF, 7° NVF, "Fovea"). The estimated peak locations of these SCE functions all cluster within a region superior and slightly nasal to the pupil center (Fig. 6). Again in this case, there is no indication that receptor orientation suddenly becomes anomalous near the foveal region. A limited number of determinations for observers SLC and SSD indicate normal appearing SCE functions at or near the fovea as well. It is therefore concluded that, for this group of amblyopic observers, subject to the sampling limitations described above, retinal receptor orientation at a range of visual field testing locations along the horizontal meridian of the visual field and including the foveal region, is relatively undisturbed. Thus, for this sample of amblyopic eyes, one must apparently look to a more proximal site within the visual system for the seat of the amblyopic visual loss.

Inferred Receptor Orientation and Visual Resolution Thresholds

SCE function measurements at the locus of fixation for observer JEC (Figs. 21, 22) indicated that receptor orientation is directed approximately toward the center of the exit pupil of this observer's right eye, for this visual field testing location. On the other hand, receptors at the locus of fixation within this observer's left eye are apparently modestly tilted away from the pupil (ca. 7° - 8°). Entoptic tests, resolution thresholds and SCE function directionalities all indicate that these determinations were directed to the foveas in both of these eyes.

Visual resolution threshold measurements at the locus of fixation in both eyes of this observer over a 4 log unit range of target luminances revealed only a modest increase in resolution thresholds for the left eye (Table 4). This difference was only apparent at the dimmer target luminances (0.23, 1.16 log photopic trolands).

These results are consistent with previous estimates of the visual resolution degradation incumbent upon a modest amount of receptor tilt. Previous estimates have been determined for receptors within isolated retina preparations (Enoch, 1971) and from psychophysical studies in which the pupil entry position of beams forming interferometric grating targets was shifted with respect to the pupil center and to the presumed location of the SCE function peak (Campbell and Gregory, 1960; Green, 1967). Thus, modest amounts of

receptor tilt at the fovea seem to result in only slight changes in resolution capability. On the other hand, gross receptor malorientation, which was not indicated within any of the observers of this study, but has previously been identified within some amblyopic eyes (Enoch, 1957; 1959a, b), is expected to have a more deleterious effect upon visual resolution (see Chapters II, III).

Visual Resolution Measurements in Amblyopic Eyes

In agreement with previous published work (e.g., Mandelbaum and Sloan, 1947), visual resolution thresholds, expressed as grating half periods in minutes of arc visual angle, were found to be lowest at central retinal regions and to increase monotonically at more peripheral testing locations (Figs. 23 - 25, Tables 1, 2).

With the exception of the smaller target size used in this study (0.5°) presented at the locus of fixation to the control observers, there was no significant trend across observers for higher resolution thresholds at the lower target luminances employed. This result may have been due to the use of interferometrically formed targets, to the target flash duration used (250 msec), to the use of a background field (e.g., Wilcox, 1932) or to some combination of these factors. For at least observer JEC, whose results may or may not be representative of the other observers, a further 1 log unit decrease of grating target luminance (to 0.23 log photopic trolands = 1.7 photopic trolands) resulted in a

clear increase in resolution target thresholds in both eyes (Table 4).

In the two amblyopic eyes of this sample, in which appreciable monocular eccentric fixation was indicated by entoptic tests, best resolution thresholds were obtained at the presumed locus of the fovea rather than at the eccentric fixation locus (Fig. 24, Table 3). This confirms similar results reported for some amblyopic observers having monocular eccentric fixation (Sandberg, 1974; Kandel and Bedell, 1976; Kirschen, 1977). However, it is apparently not true that all amblyopic eyes having monocular eccentric fixation have best resolution at the fovea (e.g., von Noorden, 1966).

The amblyopic eye resolution thresholds for interferometrically formed grating targets were found to be superior to visual acuities assessed for these eyes using Landolt ring targets. This result has previously been reported for amblyopic eyes (Gstalder and Green, 1971) and does not arise from a simple difference in luminance between the two targets. Landolt chart luminance was roughly equivalent to the middle luminance used for interferometric targets. A similar but lesser tendency for control eyes and the nonamblyopic eyes of amblyopic observers to perform superiorly for interferometrically formed targets than for Landolt targets was also noted (compare Tables 1, 2 with Appendices A, B). The discriminations required by the two types of targets differ as do the spatial characteristics of the two targets (gratings are spatially repetitive whereas Landolt rings present

spatial discontinuities). Moreover, resolution thresholds for interferometric target may have been reduced by the use of a two alternative forced choice psychophysical technique and a 71 per cent correct threshold. Whatever the reasons for the discrepancies between Landolt and interferometric acuity target resolution estimates for amblyopic eyes, the existence of such discrepancies has implications for the assessment of amblyopic eye acuities and perhaps for the etiology of amblyopia as well. Marked differences in resolution thresholds estimated for different types of targets or using different judgemental tasks suggest a localization or compartmentalization of the pathophysiological process within at least some amblyopic visual systems.

Four of the five amblyopic observers of this sample were found to have poorer interferometrically formed grating target resolution thresholds in their amblyopic eyes at _non-central_ as well as central retinal test locations. Poorer thresholds were found at both 5° and 10° from the presumed locus of the fovea in these amblyopic eyes, after correction was made for eccentric monocular fixation position in two of the observers. Previous reports of amblyopic _vs._ nonamblyopic eye resolution thresholds for peripheral and central testing locations indicate that amblyopic eye visual acuities approach or attain nonamblyopic eye levels at near peripheral retinal locations (Meur and Conreur, 1968; Kandel and Bedell, 1973; Kirschen, 1977). In two of these previous studies (Meur and Conreur, 1968; Kirschen, 1977), visual

acuity testing locations extended beyond 10°. However, previous studies have also, in general, presented their results in terms of visual acuities, rather than in minutes of arc (visual acuity = reciprocal minutes of arc of target detail). As indicated in Chapter VII, and shown in Table 2, differences in visual resolution thresholds between amblyopic and nonamblyopic eyes at peripheral retinal locations may tend to be obscured by a transformation of the data to visual acuity values.

Insofar as near peripheral resolution decrements exist in amblyopic eyes, as found for four of the five observers tested in this sample, consequences for an understanding of the pathophysiological mechanisms subserving visual resolution decrements in amblyopic eyes are indicated. That is, the present results indicate that a somewhat wider retinal region than is typically believed may be involved in the amblyopic process. Theoretical treatments of the basis of resolution deficits in amblyopic eyes may have to deal with resolution losses not confined to the immediate central retinal region. Further investigations of resolution thresholds within a larger sample of amblyopic observers extended to more peripheral retinal testing locations, seem warranted.

CHAPTER IX
CONCLUSIONS

Retinal receptor orientation, assessed as the estimated peak locations of psychophysical SCE functions determined at test locations spanning 30° of the horizontal meridian of the visual field, indicate that receptors within this region of control eyes and the amblyopic and nonamblyopic eyes of this sample of amblyopic observers tend to align toward a subregion of the exit pupil of the eye. This result confirms earlier psychophysical evidence of a photoreceptor alignment tendency toward the exit pupil of the eye in human observers.

Within one eye of this sample, an exception to this generalization was identified. For test locations spanning 45° of the horizontal visual field and 15° of the vertical field, receptors within this eye were concluded to tend to align more nearly toward the center of the retinal sphere than toward the exit pupil. Such an anomalous receptor orientation tendency has identifiable consequences for peripheral visual functioning, some of which have been identified. Preliminary electrophysiological results have indicated possible anomalies in the late phase of the electroretinogram (ERG), especially notable as a depressed light adapted c-wave, within this eye.

The sample of amblyopic eyes tested, which may not be representative of clinical amblyopia patients, revealed very little difference in estimated SCE function peak locations, or in estimated SCE function peak clustering tendencies, from either the control eyes or the nonamblyopic eyes of the same observers. Retinal receptor orientation anomalies thus seem not to play a role in the visual acuity deficits of this sample of amblyopic eyes. In addition, foveal visual resolution thresholds for a nonamblyopic observer having a displaced foveal SCE function peak location within one eye indicate that the resolution decrements to be expected from simple displacement of the SCE function peak within the pupil are not large. These results do not address the influence upon visual resolution of more severe retinal receptor orientation anomalies, which were not identified within the present sample of observers.

Visual resolution threshold profiles, assessed for a subsample of the amblyopic observers studied, revealed that in two cases of amblyopic eye monocular eccentric fixation, best resolution thresholds were obtained for targets presented at the location of the fovea, rather than at the eccentric fixation position. Furthermore, for 4 of the 5 amblyopic observers within this subsample, poorer resolution thresholds were determined for the amblyopic eyes at near peripheral as well as central retinal test locations. It is suggested that in some amblyopic eyes, subtle deficits may be found to extend beyond the central retinal region.

APPENDIX A
RESULTS OF CLINICAL MEASUREMENTS FOR AMBLYOPIC OBSERVERS

OBSERVER JEM

AGE		19
REFRACTION	OD	-1.25 sph = +0.25 x 180
	OS	-0.25 sph
LANDOLT ACUITY	OD	20/12
	OS	20/200, 20/175^{-1} PH
TROPIA/PHORIA		6 Δ ET, 1 Δ right hypertropia, far, near
MUSCLE FIELD		apparent underaction of left superior oblique
ENTOPTIC FOVEA		OD central fixation OS 5.7° - 6.9° @ 345°
AFTERIMAGE TEST		anomalous retinal correspondence
BAGOLINI LENSES		diplopia, far anomalous retinal correspondence with central suppression, near
TITMUS VECTOGRAPH		none
PULFRICH STEREO-PHENOMENON		diplopia
RANDOM DOT STEREO-GRAMS		no
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		14 OD, 16 OS
HISTORY		No known family history of strabismus or amblyopia. Left esotropia diagnosed shortly after birth. Surgery performed on muscles of both left and right eyes at age 3

OBSERVER LBP

AGE		21
REFRACTION	OD	-2.25 sph = +0.25 x 15
	OS	-9.00 sph = +0.75 x 90
LANDOLT ACUITY	OD	20/15
	OS	20/30
TROPIA/PHORIA		4 Δ XT far, increases in downgaze (A pattern) 12Δ XT near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		central fixation OU
AFTERIMAGE TEST		anomalous retinal correspondence
BAGOLINI LENSES		anomalous retinal correspondence, far anomalous retinal correspondence with suppression, near
TITMUS VECTOGRAPH		400 sec arc
PULFRICH STEREO-PHENOMENON		yes
RANDOM DOT STEREO-GRAMS		yes
SLIT LAMP		normal cornea, anterior chamber, lens OU scleral thinning on temporal globe OS
FUNDUS		large myopic crescent OS, normal OD
IOP		14 OD, 14 OS
HISTORY		No known family history of amblyopia, Esotropia diagnosed in early childhood, muscle surgery on left eye at 5 years. Subsequently patching of OD, spectacles for OS
REMARKS		Visual field appears dimmer with OS than OD

OBSERVER PMC

AGE		27
REFRACTION	OD	+2.25 sph = +.75 x 90
	OS	-2.75 sph
LANDOLT ACUITY	OD	20/35
	OS	20/12-1/2
TROPIA/PHORIA		3 Δ esophoria, far orthophoric, near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		central fixation OU
AFTERIMAGE TEST		normal retinal correspondence
BAGOLINI LENSES		slight uncrossed diplopia, far normal retinal correspondence, near
TITMUS VECTOGRAPH		800 sec arc
PULFRICH STEREO-PHENOMENON		only with filter before OS
RANDOM DOT STEREO-GRAMS		yes
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		8 OD, 12 OS
HISTORY		No known family history of strabismus or amblyopia. Amblyopia diagnosed at 11 years of age. Treated by patching OS 3-4 hours per day for 2 months
REMARKS		Visual field fades OD

OBSERVER MSM

AGE		23
REFRACTION	OD	plano
	OS	+0.50 sph = +0.50 x 90
LANDOLT ACUITY	OD	20/125, $20/100^{+1}$
	OS	20/17-1/2, $20/15^{+2}$
TROPIA/PHORIA		8 Δ ET, far
		16 Δ ET, near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		OD 1.2° - 1.8° @ 180° OS 0.4° - 0.7° @ 0°
AFTERIMAGE TEST		Anomalous retinal correspondence
BAGOLINI LENSES		Anomalous retinal correspondence, far Uncrossed diplopia, near
TITMUS VECTOGRAPH		3000 sec arc
PULFRICH STEREO-PHENOMENON		diplopia
RANDOM DOT STEREO-GRAMS		no
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		OD 17, OS 15
HISTORY		Family history of esotropia. History of accommodative esotropia since at least age 3 years. Treated with bi-focal lenses, patching routine.
REMARKS		Reports visual field dimmer with OD than OS. Small angle monocular diplopia OD.

OBSERVER BAJ

AGE		23
REFRACTION	OD	+1.25 sph
	OS	+1.00 sph = 0.25 x 175
LANDOLT ACUITY	OD	20/17-1/2
	OS	20/25 $20/20^{+2}$ PH
TROPIA/PHORIA		4 Δ ET, far 8 Δ ET, Near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		central fixation OU
AFTERIMAGE TEST		anomalous retinal correspondence
BAGOLINI LENSES		anomlaous retinal corresondence far, near
TITMUS VECTOGRAPH		3000 sec arc
PULFRICH STEREO-PHENOMENON		only with filter before OS
RANDOM DOT STEREO-GRAMS		no
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OD, decreased pigmentation ca. 2 disc diameters inferior to macula OS
IOP		13 OD, 12 OS
HISTORY		History of esotropia with amblyopia on father's side. Treated by patching OD, lenses. Probable accommodative component.

OBSERVER SLC

AGE		20
REFRACTION	OD	plano = 0.25 x 0
	OS	+0.50 sph
LANDOLT ACUITY	OD	20/17-1/2
	OS	20/175
TROPIA/PHORIA		6 Δ ET far and near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		OD central fixation OS 0.5° - 0.6° @ 10°
AFTERIMAGE TEST		anomalous retinal correspondence
BAGOLINI LENSES		anomalous retinal correspondence with intermittant suppression of OS
TITMUS VECTOGRAPH		none
PULFRICH STEREO-PHENOMENON		diplopia
RANDOM DOT STEREO-GRAMS		no
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		OD 16, OS 14
HISTORY		No known family history of strabismus or amblyopia. Right esotropia diagnosed at 1-2 years old. Treated with patching OD.
REMARKS		Nasal visual field OS appears dim.

OBSERVER SSD

AGE		21
REFRACTION	OD	-1.50 sph = +0.50 x 90
	OS	+1.00 sph = +0.25 x 90
LANDOLT ACUITY	OD	20/30
	OS	$20/60, 20/50^{+2}$
TROPIA/PHORIA		4 Δ ET, far Alternating hypertropia (double vertical deviation) both far and near
MUSCLE FIELD		apparent underactive left inferior oblique, left inferior rectus
ENTOPTIC FOVEA		OD 0.4° - 1.4°, variable axis OS 0.7° - 0.9° @ 320°
AFTERIMAGE TEST		normal retinal correspondence
BAGOLINI LENSES		anomalous retinal correspondence, far and near, intermittant suppression of OD
TITMUS VECTOGRAPH		none
PULFRICH STEREO-PHENOMENON		yes
RANDOM DOT STEREO-GRAMS		none
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		15 OD, 14 OS
HISTORY		Family history of esotropia. Apparent congenital esotropia. Bilateral medial recession performed at 18 months of age. Subsequently treated with patching, atropine penalization of OS. Postoperatively developed alternating hypertropia. At age 17, cosmetic surgery on left lateral rectus, inferior oblique to correct residual deviation.

APPENDIX B
RESULTS OF CLINICAL MEASUREMENTS FOR CONTROL OBSERVERS AND FOR JEC

OBSERVER SBS

AGE		33
REFRACTION	OD	+0.50 sph = +0.50 x 104
	OS	+0.25 sph = +0.25 x 80
LANDOLT ACUITY	OD	20/17-1/2
	OS	20/17-1/2
TROPIA/PHORIA		1 Δ esophoria far, 2 Δ exophoria near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		OD central fixation OS 0.6° - 0.9° @ 25°
AFTERIMAGE TEST		normal retinal correspondence
BAGOLINI LENSES		normal retinal correspondence
TITMUS VECTOGRAPH		40 sec arc
PULFRICH STEREO-PHENOMENON		yes
RANDOM DOT STEREO-GRAMS		yes
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		normal OU
IOP		10 OD 14 OS

OBSERVER MAP

AGE		22
REFRACTION	OD	-1.00 sph
	OS	-0.75 sph
LANDOLT ACUITY	OD	20/17-1/2, $20/15^{+3}$
	OS	20/15
TROPIA/PHORIA		4 Δ esophoria far, orthophoric near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		central fixation OU
AFTERIMAGE TEST		normal retinal correspondence
BAGOLINI LENSES		normal retinal correspondence
TITMUS VECTOGRAPH		40 sec arc
PULFRICH STEREO-PHENOMENON		yes
RANDOM DOT STEREO GRAMS		yes
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		nevis in macular region OD, normal OS
IOP		16 OD, 16 OS
REMARKS		anisocoria, left pupil larger

OBSERVER JEC

AGE		24
REFRACTION	OD	-3.25 sph
	OS	-1.50 sph = +0.50 x 93
LANDOLT ACUITY	OD	$20/15^{-1}$
	OS	$20/15^{-2}$
TROPIA/PHORIA		6 Δ esophoria far, 12 Δ exophoria near
MUSCLE FIELD		normal
ENTOPTIC FOVEA		central fixation OU
AFTERIMAGE TEST		normal retinal correspondence
BAGOLINI LENSES		normal retinal correspondence
TITMUS VECTOGRAPH		40 sec arc
PULFRICH STEREO-PHENOMENON		yes, also reports spontaneous Pulfrich effect, neutralized by 0.2 ND before OD
RANDOM DOT STEREO-GRAMS		yes
SLIT LAMP		cornea, anterior chamber, lens normal OU
FUNDUS		tesselated appearance OU, myopic crescents OU, possible pigment epithelial changes around macula and near disc OD
IOP		16 OD, 16 OS

APPENDIX C
ESTIMATED SCE FUNCTION PEAK LOCATIONS

Key

Key

A	Amblyopic Eye
D	Nonamblyopic eye of amblyopic observer
C	Control Eye
NVF	Nasal visual field
TVF	Temporal visual field
IVF	Inferior visual field
N	Nasal from pupil center (mm)
T	Temporal from pupil center (mm)
I	Inferior to pupil center (mm)
S	Superior to pupil center (mm)
"Fovea"	Indicates SCE functions determined at the visual field location corresponding to the position of the entoptic fovea. The visual field location of the entoptic fovea with respect to the fixation target used is given in parentheses.

Observer JEM, Right Eye (D)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.74N	(0.30N - 1.16N)	0.96S	(1.28S - 0.71S)
5° NVF	0.74N	(0.60N - 0.89N)	0.74S	(0.92S - 0.59S)
10° NVF	1.14N	(0.92N - 1.42N)	0.86S	(1.26S - 0.59S)
20° NVF	1.84N	(1.47N - 2.70N)	0.81S	(1.10S - 0.58S)
5° TVF	0.62N 0.50N	(0.36N - 0.98N) (0.34N - 0.69N)	0.79S 1.03S	(0.99S - 0.62S) (1.27S - 0.84S)
10° TVF	0.98N	(0.57N - 1.34N)	1.01S	(1.67S - 0.65S)

Observer JEM, Left Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	1.49N	(1.22N - 1.90N)	0.10S	(0.43S - 0.24I)
"Fovea" (5.5° @ 345°)[#]	0.51N	(0.34N - 0.71N)	0.92S	(1.26S - 0.69S)
5° NVF	0.58N 0.61N	(0.25N - 1.12N) (0.28N - 1.16N)	1.14S	(1.57S - 0.89S)
7° NVF	0.05N	(0.17T - 0.30N)	0.60S	(0.99S - 0.34S)
10° NVF	0.01T	(0.20T - 0.18N)	1.06S	(1.69S - 0.70S)
20° NVF	0.13T	(0.54T - 0.21N)	0.37S	(0.77S - 0.11S)
5° TVF	0.86N	(0.59N - 1.24N)	0.19I	(0.02S - 0.37I)

[#]Estimated from the position of the Maxwell spot centroid relative to the fixation locus.

Observer LBP, Right Eye (D)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.85N	(0.70N - 1.01N)	1.31S	(1.62S - 1.05S)
	0.90N	(0.70N - 1.14N)	1.59S	(1.90S - 1.36S)
5° NVF	0.43N	(0.29N - 0.61N)	0.95S	(1.14S - 0.73S)
	0.51N	(0.36N - 0.68N)		
10° NVF	0.40N	(0.05N - 0.71N)	0.92S	(1.18S - 0.72S)
20° NVF	0.31T	(0.46T - 0.18T)	0.39S	(0.65S - 0.17S)
5° TVF	0.90N	(0.67N - 1.13N)	0.75S	(0.95S - 0.56S)
10° TVF	1.06N	(0.82N - 1.31N)	0.60S	(0.87S - 0.38S)
	1.18N	(0.95N - 1.40N)	0.25S	(0.53S - 0.13S)

Observer LBP, Left Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	1.00T 1.09T	(1.23T - 0.81T) (1.62T - 0.72T)	1.40I	(1.26I - 1.57I)
2-1/2° NVF	0.25T	(0.47T - 0.06T)	1.31I	(1.15I - 1.49I)
5° NVF	0.64N	(0.38N - 0.91N)	1.33I	(1.15I - 1.53I)
10° NVF	1.52N	(1.30N - 1.82N)	1.29I	(1.10I - 1.53I)
20° NVF	0.95N 1.22N	(0.63N - 1.55N) (0.88N - 1.83N)	0.82I	(0.36I - 1.15I)
5° TVF	1.08T 1.20T	(1.71T - 0.74T) (1.44T - 1.02T)	1.70I	(2.07I - 1.45I)
10° TVF	0.18T	(0.55T - 0.19N)	1.39I	(2.02I - 1.02I)

Observer PMC, Right Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.46N	(0.30N - 0.61N)	0.64S	(0.85S - 0.43S)
5° NVF	0.45N	(0.30N - 0.60N)	0.89S	(1.06S - 0.71S)
10° NVF	0.10N 0.17N	(0.05T - 0.26N) (0.00 - 0.36N)	0.64S	(0.97S - 0.06S)
20° NVF	1.06N	(0.81N - 1.42N)	0.40S	(0.84S - 0.10S)
5° TVF	0.92N	(0.70N - 1.15N)	0.28S	(0.38S - 0.18S)
10° TVF	0.41N 0.21N	(0.21N - 0.66N) (0.02N - 0.42N)	0.46S	(0.73S - 0.19S)
10° IVF	0.25N	(o.01N - 0.55N)	0.85S	(1.24S - 0.60S)

Observer PMC, Left Eye (D)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.63N 0.49N	(0.42N - 0.86N) (0.34N - 0.66N)	0.09I	(0.12S - 0.32I)
5° NVF	1.36N	(1.12N - 1.66N)	0.12S	(0.21S - 0.00)
10° NVF	2.03N	(1.78N - 2.41N)	0.18S	(0.35S - 0.03S)
15° NVF	2.91N	(2.29N - *)	0.18S	(0.70S - 0.23I)
20° NVF	3.20N	(2.08N - *)	0.17S	(0.85S - 0.33I)
5° TVF	1.01T	(1.12T - 0.87T)	0.10I	(0.08S - 0.28I)
10° TVF	1.66T	(3.39T - 0.86T)	0.41I	(0.24I - 0.60I)
25° TVF	4.60T	(* - 2.45T)		
10° IVF	0.21T	(0.47T - 0.00)	1.17I	(0.93I - 1.47I)
15° IVF	0.34T	(1.14T - 0.08N)	1.99I	(1.63I - 2.58I)

*Boundary of confidence interval falls beyond the pupil.

Observer MSM, Right Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	1.97N	(1.75N - 2.28N)	0.36S	(0.66S - 0.05S)
"Fovea" (1.96° NVF)	1.94N	(1.52N - 3.38N)	0.16S	(0.61S - 0.19I)
10° NVF	1.84N	(1.56N - 2.25N)	0.61S	(0.94S - 0.38S)
20° NVF	1.39N	(1.20N - 1.63N)	0.69S	(1.62S - 0.12S)
10° TVF	1.30N	(1.12N - 1.53N)	0.06I	(0.14S - 0.30I)

Observer MSM, Left Eye (D)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	1.97N	(1.73N - 2.33N)	0.66S	(1.01S - 0.37S)
"Fovea" (1.0° NVF)	1.88N	(1.51N - 2.58N)	0.70S	(1.10S - 0.43S)
10° NVF	1.86N	(1.67N - 2.12N)	1.06S	(1.29S - 0.86S)
20° NVF	1.15N	(0.93N - 1.45N)	0.27S	(0.53S - 0.04S)
5° TVF	1.11N	(0.99N - 1.23N)	0.28S	(0.52S - 0.06S)
10° TVF	0.87N	(0.65N - 1.06N)	0.20S	(0.40S - 0.03S)

Observer BAJ, Right Eye (D)

	Horiontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.64T	(1.05T - 0.23T)	0.13S	(0.85S - 0.42I)
10° NVF	0.27T	(0.41T - 0.13T)	0.16S	(0.30S - 0.03S)
20° NVF	1.16T	(1.70T - 0.80T)	0.68S	(1.20S - 0.38S)
10° NVF	0.07T	(0.31T - 0.14N)	0.03S	(0.33S - 0.26I)

Observer BAJ, Left Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.31N	(0.04N - 0.66N)	0.14I	(0.28S - 0.57I)
10° NVF	0.22T	(0.34T - 0.11T)	0.06I	(0.22S - 0.38I)
20° NVF	1.05T	(1.32T - 0.83T)	0.43S	(0.87S - 0.15S)
10° TVF	0.69N	(0.45N - 0.98N)	0.01I	(o.26S - 0.55I)

Observer SLC, Right Eye (D)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.64N	(0.33N - 0.98N)	0.44S	(0.97S - 0.09S)

Observer SLC, Left Eye (A)

Fixation	0.67N	(0.16N - 0.58N)	0.35I	(0.16I - 0.57I)
"Fovea" (0.55° NVF)	0.57N	(0.34N - 0.79N)	0.58I	(0.28I - 0.81I)

Observer SSD, Right Eye (A)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.52N	(0.22N - 1.00N)	0.81I	(0.43I - 1.58I)

Observer SSD, Left Eye (D)

Fixation	0.83N	(0.67N - 1.03N)	0.26I	(0.07I - 0.48I)
	1.19N	(0.58N - *)	0.49I	(0.06S - 1.02I)
"Fovea" (1.32° @ 330°)	1.07N	(0.79N - 1.46N)	0.26I	(0.06S - 0.68I)

*Boundary of confidence interval falls beyond the pupil.

Observer SBS, Right Eye (C)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.36N	(0.04N - 0.64N)	0.42I	(0.01I - 1.18I)
5° NVF	0.09N	(0.06T - 0.24N)	0.20I	(0.03I - 0.41I)
10° NVF	0.08T	(0.27T - 0.10N)	0.74I	(0.50I - 1.02I)
20° NVF	0.98N	(0.74N - 1.28N)	0.29I	(0.15I - 0.45I)
5° TVF	0.25T	(0.04T - 0.51T)	0.25I	(0.04I - 0.51I)
10° TVF	0.95T	(0.64T - 1.39T)	0.48I	(0.27I - 0.74I)

Observer SBS, Left Eye (C)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.34N	(0.02T - 0.85N)	0.11I	(0.13S - 0.36I)
	0.48N	(0.12T - 1.01N)	0.03I	(0.49S - 0.55I)
"Fovea" (0.62° @ 40°)	0.36N	(0.04N - 0.83N)	0.30I	(0.01I - 0.50I)
5° NVF	0.15N	(0.06T - 0.37N)	0.15I	(0.04I - 0.29I)
10° NVF	0.17T	(0.47T - 0.10N)	0.10I	(0.12S - 0.33I)
	0.01T	(0.16T - 0.15N)	0.53I	(0.36I - 0.70I)
20° NVF	1.38N	(1.06N - 1.90N)	0.81I	(0.57I - 1.16I)
	1.10N	(0.72N - 1.71N)		
5° TVF	0.44N	(0.36N - 0.53N)	0.14I	(0.16S - 0.47I)
	0.39N	(0.20N - 0.62N)	0.03I	(0.16S - 0.09I)
10° TVF	0.03N	(0.23T - 0.16N)	0.46I	(0.34I - 0.57I)
35° TVF[#]	1.57N	(0.97N - 3.15N)	0.30I	(0.01I - 0.55I)

[#]Previously reported in Bedell and Enoch (1978).

Observer MAP, Right Eye (C)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.51N	(0.23N - 0.76N)	0.10I	(0.24S - 0.47I)
5° NVF	0.57N	(0.43N - 0.72N)	0.01S	(0.17S - 0.17I)
10° NVF	0.87N	(0.51N - 1.12N)	0.02S	(0.30S - 0.28I)
20° NVF	0.02T	(0.64T - 0.56N)	0.36I	(0.04I - 0.85I)
5° TVF	0.06T	(0.17T - 0.06N)	0.03I	(0.08S - 0.15I)
10° TVF	0.56T	(0.79T - 0.32T)	0.02I	(0.21S - 0.26I)

Observer MAP, Left Eye (C)

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	0.87T	(1.09T - 0.58T)	0.35S	(0.65S - 0.12S)
5° NVF	0.11T	(0.35T - 0.11N)	0.45S	(0.64S - 0.29S)
10° NVF	0.93N	(0.54N - 1.24N)	0.13S	(0.41S - 0.13I)
20° NVF	0.22N	(0.02T - 0.47N)	0.38I	(0.21I - 0.57I)
5° TVF	0.79T	(0.96T - 0.63T)	0.07S	(0.25S - 0.10I)
10° TVF	0.11N	(0.24T - 0.37N)	0.36I	(0.02S - 1.00I)

Observer JEC, Right Eye

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	1.09T	(1.43T - 0.79T)	0.48I	(0.13I - 0.77I)
	1.17T	(1.55T - 0.83T)	0.45I	(0.16I - 0.91I)
5° NVF	0.19T	(0.37T - 0.02T)	0.05I	(0.08S - 0.18I)
10° NVF	0.58N	(0.30N - 0.99N)	0.12I	(0.08S - 0.32I)
	0.71N	(0.40N - 1.20N)		
20° NVF	0.76N	(0.39N - 1.31N)	0.27S	(1.33S - 0.37I)
5° TVF	1.52T	(1.85T - 1.28T)	1.21I	(0.98I - 1.44I)
10° TVF	2.80T	(* - 2.09T)	1.07I	(0.72I - 1.59I)
	2.30T	(3.63T - 1.80T)		

*Boundary of confidence interval falls beyond the pupil.

Observer JEC, Left Eye

	Horizontal		Vertical	
	Peak Location	99 Per cent Confidence Interval	Peak Location	99 Per cent Confidence Interval
Fixation	2.45T	(* - 1.79T)	1.74I	(0.92I - 2.86I)
	1.73T	(2.02T - 1.53T)	2.27I	(1.83I - 3.37I)
5° NVF	0.78T	(0.99T - 0.58T)	1.03I	(0.90I - 1.15I)
10° NVF	0.76N	(0.55N - 1.00N)	0.80I	(0.63I - 0.97I)
20° NVF	0.14N	(0.79N - 1.71N)	0.02I	(0.25S - 0.29I)
5° TVF	1.75T	(2.42T - 1.41T)	2.08I	(1.68I - 2.93I)
			2.19I	(1.88I - 2.70I)
10° TVF	1.14T	(1.54T - 0.86T)	1.71I	(1.38I - 2.29I)
	1.03T	(1.72T - 0.40T		
35° TVF	0.62T	(1.08T - 0.14T)	0.67I	(0.27I - 1.54I)
	0.77T	(1.04T - 0.49T)	0.81I	(0.53I - 1.17I)

*Boundary of confidence interval falls beyond the pupil.

Definition of 99 Per Cent Confidence Intervals and 98 Per Cent Confidence Rectangles for the Location of the SCE Function Peaks

Confidence intervals were calculated using the formula (Williams, 1959)

$$CI = x_{max}\left[\frac{(1-g_{23}) \pm \sqrt{(1-g_{23})^2 - (1-g_{22})(1-g_{33})}}{(1-g_{33})}\right].$$

where CI = confidence interval.

x_{max} = SCE function peak location estimated as $(-b_2/2b_3)$ from the fitted parabola

$$y = \log \eta = b_1 + b_2x + b_3x^2.$$

$$g_{ij} = \frac{(t^2_{df=n-3})(s^2)(v_{ij})}{(b_i)(b_j)}$$

in which t = value from Student's t distribution corresponding to P=0.01

and having (n-3) degrees of freedom.

n = the number of (x,y) data pairs used in fitting the parabola.

b_i, b_j = the appropriate coefficients of the fitted parabola.

s^2 = the mean square residual error about the fitted parabola.

v_{ij} = the appropriate element of the (3 x 3) X inverse matrix calculated as a part of the fitting procedure.

Using this formula, 99 per cent confidence intervals were calculated for SCE function locations estimated from horozintal and vertical traverses of the pupil at each visual field testing location. The probability that each horizontal or vertical confidence interval about the estimated SCE function peak location includes the location of the true SCE function peak, within that meridian, is 0.99. Thus, a confidence rectangle, defined by both the horizontally and vertically defined confidence intervals, contains the true SCE function peak location for a given visual field test location with a probability of $(0.99)(0.99) = 0.98$.

Minimum confidence estimates about differences in estimated SCE function peak locations for different visual field testing locations can be defined when confidence rectangles about each estimated peak location do not overlap. Since each confidence rectangle contains the true SCE function peak location for a specified visual field test location with probability of 0.98, the probability that each of two nonoverlapping confidence rectangles contain the true SCE function peaks, i.e., that the true peaks differ in location, is $(0.98)(0.98) = 0.96$.

This analysis assumes that true SCE function peak locations at different retinal regions are independent, which is almost certainly not true, especially for nearby retinal regions. Hence, confidence statements based upon this analysis must be conservative. Moreover, this analysis does not take into account observer alignment or other systematic

errors in data collection. These errors are estimated to be small relative to observed differences in estimated SCE function peak locations.

APPENDIX D
ESTIMATED SCE FUNCTION DIRECTIONALITY

Observer JEM, Right Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensivitity Half Width (mm)
Fixation	0.053 ± 0.031	2.38	0.049 ± 0.014	2.48
5° NVF	0.085 ± 0.013	1.88	0.090 ± 0.014	1.83
10° NVF	0.067 ± 0.015	2.12	0.088 ± 0.036	1.85
20° NVF	0.077 ± 0.039	1.98	0.107 ± 0.040	1.68
5° TVF	0.071 ± 0.020 0.077 ± 0.015	2.06 1.98	0.066 ± 0.013 0.098 ± 0.026	2.14 1.75
10° TVF	0.59 ± 0.027	2.26	0.067 ± 0.024	2.12

Observer JEM, Left Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.075 ± 0.026	2.00	0.075 ± 0.029	2.00
"Fovea" (5.5° @ 345°)	0.075 ± 0.014	2.00	0.095 ± 0.033	1.78
5° NVF	0.082 ± 0.032 0.083 ± 0.035	1.92 1.90	0.093 ± 0.033	1.80
7° NVF	0.100 ± 0.028	1.73	0.082 ± 0.026	1.92
10° NVF	0.094 ± 0.021	1.82	0.079 ± 0.026	1.95
20° NVF	0.068 ± 0.031	2.10	0.075 ± 0.027	2.00
5° TVF	0.087 ± 0.024	1.86	0.076 ± 0.015	2.02

Observer LBP, Right Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.051 ± 0.009	2.43	0.049 ± 0.017	2.48
	0.052 ± 0.011	2.41	0.051 ± 0.015	2.43
5° NVF	0.085 ± 0.015	1.88	0.067 ± 0.018	2.12
	0.078 ± 0.014	1.96		
10° NVF	0.055 ± 0.019	2.37	0.070 ± 0.013	2.10
20° NVF	0.058 ± 0.007	2.28	0.055 ± 0.012	2.37
5° TVF	0.063 ± 0.018	2.19	0.058 ± 0.012	2.28
10° TVF	0.054 ± 0.013	2.36	0.052 ± 0.011	2.41
	0.074 ± 0.022	2.02	0.071 ± 0.020	2.06

Observer LBP, Left Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.065 ± 0.013	2.15	0.062 ± 0.012	2.20
	0.048 ± 0.018	2.50		
2-1/2° NVF	0.069 ± 0.017	2.09	0.071 ± 0.014	2.06
5° NVF	0.063 ± 0.017	2.19	0.057 ± 0.014	2.30
10° NVF	0.058 ± 0.018	2.28	0.059 ± 0.011	2.26
20° NVF	0.038 ± 0.015	2.81	0.033 ± 0.014	3.02
	0.043 ± 0.014	2.65		
5° TVF	0.066 ± 0.032	2.14	0.057 ± 0.017	2.30
	0.060 ± 0.009	2.24		
10° TVF	0.039 ± 0.016	2.78	0.037 ± 0.012	2.85

Observer PMC, Right Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.066 ± 0.011	2.17	0.066 ± 0.015	2.17
5° NVF	0.095 ± 0.016	1.78	0.090 ± 0.021	1.83
10° NVF	0.081 ± 0.016 0.086 ± 0.018	1.93 1.87	0.076 ± 0.036	1.99
20° NVF	0.070 ± 0.021	2.07	0.070 ± 0.026	2.07
5° TVF	0.091 ± 0.029	1.82	0.109 ± 0.014	1.66
10° TVF	0.062 ± 0.012 0.070 ± 0.017	2.20 2.07	0.067 ± 0.019	2.12
10° IVF	0.091 ± 0.030	1.82	0.074 ± 0.031	2.02

Observer PMC, Left Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.072 ± 0.021 0.058 ± 0.011	2.04 2.28	0.047 ± 0.012	2.53
5° NVF	0.083 ± 0.025	1.90	0.079 ± 0.017	1.95
10° NVF	0.075 ± 0.022	2.00	0.072 ± 0.019	2.04
15° NVF	0.034 ± 0.027	2.98	0.047 ± 0.022	2.53
20° NVF	0.034 ± 0.031	2.98	0.049 ± 0.029	2.48
5° TVF	0.070 ± 0.012	2.07	0.089 ± 0.019	1.84
10° TVF	0.056 ± 0.021	2.32	0.042 ± 0.007	2.68
25° TVF	0.031 ± 0.058	3.12		
10° IVF	0.068 ± 0.022	2.10	0.064 ± 0.015	2.17
15° IVF	0.045 ± 0.027	2.59	0.033 ± 0.014	3.02

Observer MSM, Right Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.077 ± 0.016	1.98	0.063 ± 0.020	2.19
"Fovea" (1.96° NVF)	0.059 ± 0.039	2.26	0.055 ± 0.027	2.34
10° NVF	0.088 ± 0.025	1.85	0.097 ± 0.029	1.76
20° NVF	0.079 ± 0.016	1.95	0.078 ± 0.060	1.96
10° TVF	0.085 ± 0.021	1.91	0.081 ± 0.023	1.93

Observer MSM, Left Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.068 ± 0.018	2.14	0.050 ± 0.016	2.45
"Fovea" (1.0° NVF)	0.068 ± 0.026	2.14	0.073 ± 0.025	2.03
10° NVF	0.078 ± 0.016	1.96	0.082 ± 0.023	1.91
20° NVF	0.081 ± 0.020	1.93	0.086 ± 0.026	1.87
5° TVF	0.101 ± 0.016	1.73	0.096 ± 0.027	1.77
10° TVF	0.085 ± 0.022	1.88	0.097 ± 0.023	1.76

Observer BAJ, Right Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.041 ± 0.017	2.71	0.042 ± 0.026	2.68
10° NVF	0.082 ± 0.012	1.92	0.087 ± 0.015	1.86
20° NVF	0.057 ± 0.026	2.30	0.075 ± 0.028	2.00
10° TVF	0.104 ± 0.029	1.70	0.111 ± 0.038	1.65

Observer BAJ, Left Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.063 ± 0.022	2.19	0.055 ± 0.025	2.34
10° NVF	0.101 ± 0.015	1.73	0.094 ± 0.034	1.79
20° NVF	0.069 ± 0.017	2.09	0.062 ± 0.024	2.20
10° TVF	0.077 ± 0.022	1.98	0.083 ± 0.028	1.90

Observer SLC, Right Eye (D)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.051 ± 0.018	2.43	0.051 ± 0.024	2.43

Observer SLC, Left Eye (A)

Fixation	0.077 ± 0.011	1.98	0.073 ± 0.018	2.03
"Fovea" (0.55° NVF)	0.075 ± 0.019	2.00	0.076 ± 0.023	1.99

Observer SSD, Right Eye (A)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.071 ± 0.028	2.06	0.053 ± 0.023	2.38

Observer SSD, Left Eye (D)

Fixation	0.078 ± 0.019	1.96	0.078 ± 0.019	1.96
	0.066 ± 0.063	2.14	0.038 ± 0.020	2.81
"Fovea" (1.32° @ 330°)	0.070 ± 0.029	2.07	0.067 ± 0.028	2.12

Observer SBS, Right Eye (C)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.057 ± 0.017	2.30	0.042 ± 0.017	2.68
5° NVF	0.106 ± 0.021	1.69	0.103 ± 0.026	1.71
10° NVF	0.081 ± 0.019	1.93	0.079 ± 0.020	1.95
20° NVF	0.054 ± 0.015	2.36	0.052 ± 0.009	2.41
5° TVF	0.097 ± 0.027	1.76	0.107 ± 0.031	1.68
10° TVF	0.058 ± 0.011	2.28	0.061 ± 0.015	2.22

Observer SBS, Left Eye (C)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.046 ± 0.016	2.56	0.058 ± 0.014	2.28
	0.047 ± 0.025	2.53	0.041 ± 0.019	2.71
"Fovea" (0.62° @ 40°)	0.064 ± 0.026	2.17	0.067 ± 0.024	2.12
5° NVF	0.105 ± 0.026	1.69	0.085 ± 0.019	1.88
10° NVF	0.058 ± 0.019	2.28	0.066 ± 0.017	2.14
	0.062 ± 0.012	2.20	0.060 ± 0.011	2.24
20° NVF	0.041 ± 0.021	2.71	0.082 ± 0.032	1.92
	0.057 ± 0.024	2.30		
5° TVF	0.092 ± 0.021	1.81	0.087 ± 0.013	1.86
	0.090 ± 0.009	1.83	0.074 ± 0.026	2.02
10° TVF	0.080 ± 0.021	1.94	0.067 ± 0.008	2.12
35° TVF	0.032 ± 0.019	3.07	0.050 ± 0.014	2.45

Observer MAP, Right Eye (C)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.054 ± 0.015	2.36	0.054 ± 0.021	2.36
5° NVF	0.065 ± 0.010	2.15	0.080 ± 0.018	1.94
10° NVF	0.064 ± 0.023	2.17	0.057 ± 0.019	2.30
20° NVF	0.051 ± 0.033	2.43	0.051 ± 0.024	2.43
5° TVF	0.091 ± 0.013	1.82	0.083 ± 0.013	1.90
10° TVF	0.060 ± 0.015	2.24	0.061 ± 0.018	2.22

Observer MAP, Left Eye (C)

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.066 ± 0.021	2.14	0.056 ± 0.015	2.32
5° NVF	0.068 ± 0.018	2.10	0.077 ± 0.014	1.98
10° NVF	0.056 ± 0.023	2.32	0.062 ± 0.019	2.20
20° NVF	0.043 ± 0.010	2.64	0.046 ± 0.009	2.56
5° TVF	0.067 ± 0.011	2.12	0.083 ± 0.017	1.90
10° TVF	0.059 ± 0.017	2.26	0.064 ± 0.031	2.17

Observer JEC, Right Eye

	Horizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.047 ± 0.018	2.53	0.046 ± 0.014	2.56
	0.047 ± 0.019	2.53	0.049 ± 0.019	2.48
5° NVF	0.113 ± 0.021	1.63	0.095 ± 0.015	1.78
10° NVF	0.067 ± 0.015	2.12	0.077 ± 0.018	1.98
	0.071 ± 0.022	2.06		
20° NVF	0.047 ± 0.015	2.53	0.059 ± 0.039	2.56
5° TVF	0.073 ± 0.021	2.03	0.069 ± 0.020	2.09
10° TVF	0.033 ± 0.020	3.02	0.038 ± 0.012	2.81
	0.040 ± 0.021	2.74		

Observer JEC, Left Eye

	Hozizontal		Vertical	
	rho	Half Sensitivity Half Width (mm)	rho	Half Sensitivity Half Width (mm)
Fixation	0.046 ± 0.067	2.56	0.049 ± 0.043	2.48
	0.061 ± 0.020	2.22	0.038 ± 0.020	2.81
5° NVF	0.091 ± 0.019	1.82	0.096 ± 0.016	1.77
10° NVF	0.063 ± 0.014	2.19	0.091 ± 0.019	1.82
20° NVF	0.051 ± 0.020	2.43	0.048 ± 0.012	2.50
5° TVF	0.061 ± 0.027	2.22	0.054 ± 0.023	2.36
			0.054 ± 0.016	2.36
10° TVF	0.053 ± 0.017	2.38	0.066 ± 0.026	2.14
	0.053 ± 0.034	2.38		
35° TVF	0.053 ± 0.022	2.38	0.061 ± 0.030	2.22
	0.042 ± 0.010	2.68	0.072 ± 0.021	2.04

REFERENCES

Aguilar, M. and Plaza, A., Efecto Stiles-Crawford en vision extrafoveal, Anales de la Real Soc. Española de Fis. y Quim. 50, 119-126, 1954.

Alpern, M. and Benson, D. J., Directional sensitivity of the pupillomotor photoreceptors, Amer. J. Optom. and Arch. Amer. Acad. Optom. 30, 569-580, 1953.

Alpern, M., Petrauskas, R. R., Sandall, G. S. and Vorenkamp, R. J., Recent experiments on the physiology of strabismus amblyopia, Amer. Orthoptic J. 17, 62-72, 1967.

Ames, A. and Glidden, C., Ocular measurement, Trans. of the Section of Opthalmol., 102-175, 1928.

Armington, J. C., Pupil entry and the human electroretinogram, J. Opt. Soc. Amer. 57, 838-839, 1967.

Bagolini, B., Sensorial anomalies in strabismus, Doc. Ophthal. 41, 1-22, 1976.

Bailey, J. E., The orientation properties of retinal rods, Optometric Weekly, 63(19), 32-33, 1972.

Bailey, J. E., Directional sensitivity of retinal receptors, Ph.D. Dissertation, Indiana University, 1974.

Baker, F. H., Grigg, P. and von Noorden, G. K., Effects of visual deprivation and strabismus on the response of neurons in the visual cortex of the monkey, including studies on the striate and prestriate cortex in the normal animal, Brain Res. 66, 185-208, 1974.

Baker, H. D., The course of forveal light adaptation measured by the threshold intensity increment, J. Opt. Soc. Amer. 39, 172-179, 1949.

Barer, R., Refractometry and interferometry of living cells, J. of the Opt. Soc. of Amer. 47, 545-556, 1957.

Baylor, D. A. and Fettiplace, R., Light path and photon capture in turtle photoreceptors, J. Physiol. 248, 433-464, 1975.

Beck, L. H., A functional interpretation of the Stiles-Crawford effect, J. Opt. Soc. Amer. 43, 924, 1953.

Bedell, H. E., Stiles-Crawford effect and light adaptation in a severe strabismic amblyope, Masters Thesis, Rensselaer Polytechnic Institute, 1974.

Bedell, H. E. and Enoch, J. M., A study of the Stiles-Crawford (S-C) function at 35° in the temporal field and the stability of the foveal S-C function peak over time, J. Opt. Soc. Amer., in press, 1978.

Benson, W. E., Kolker, A. E., Enoch, J. M., vanLoo, J. A. and Honda, Y., Best's vitelliform macular dystrophy, Amer. J. Ophthalmol. 79, 59-66, 1975.

Blank, K., Provine, R. R. and Enoch, J. M., Shift in the peak of the photopic Stiles-Crawford function with marked accommodation, Vision Res. 15, 499-507, 1975.

Boer, P. and Hofstetter, H. W., An entoptic method for the measurement of eccentric fixation in amblyopia ex anopsia, Amer. J. Optom. and Arch. Amer. Acad. Optom. 49, 417-422, 1972.

Bonds, A. B. and MacLeod, D. I. A., A displaced Stiles-Crawford effect associated with an eccentric pupil, Invest. Ophthal., in press, 1978.

Boynton, R. M. and Gordon, J., Bezold-Brücke hue shift measured by color-naming technique, J. Opt. Soc. Amer. 55, 78-86, 1965.

Brindley, G. S., The effects on colour vision of adaptation to very bright lights, J. Physiol. 122, 332-350, 1953.

Brindley, G. S., The deformation phosphene and the funnelling of light into rods and cones, J. Physiol. 147, 24-25P, 1959.

Brindley, G. S. and Rushton, W. A. H., The colour of monochromatic light when passed into the human retina from behind, J. Physiol. 147, 204-208, 1959.

Burian, H. M., Discussion of paper by Fankhauser and Röhler, Doc. Ophthal. 23, 185-187, 1967a.

Burian, H. M., The behavior of the amblyopic eye under reduced illumination and the theory of functional amblyopia, Doc. Ophthal. 23, 189-202, 1967b.

Burian, H. M. and von Noorden, G. K., Binocular Vision and Ocular Motility, Mosby, St. Louis, 1974, pp. 221-222.

Campbell, F. W., A retinal acuity direction effect, J. Physiol. 144, 25-26P, 1958.

Campbell, F. W. and Gregory, A. H., The spatial resolving power of the human retina with oblique incidence, J. Opt. Soc. Amer. 50, 831, 1960.

Campos, E. C., Bedell, H. E., Enoch, J. M. and Fitzgerald, C. R., Retinal receptive field-like properties and Stiles-Crawford effect in a patient with traumatic choroidal rupture, Doc. Ophthal., in press, 1978.

Coble, J. R. and Rushton, W. A. H., Stiles-Crawford effect and the bleaching of cone pigments, J. Physiol. 217, 231-242, 1971.

Craik, K. J. W., Transmission of light by the eye media, J. Physiol. 98, 179-184, 1940.

Crawford, B. H., The luminous efficiency of light entering the eye pupil at different points and its relation to brightness threshold measurements, Proc. Roy. Soc. Lond. B124, 81-96, 1937.

Crawford, B. H., The Stiles-Crawford effects and their significance in vision, in Jameson, D. and Hurvich, L. M. (eds.) Visual Psychophysics, Handbook of Sensory Physiology, Vol. VII/4, Springer-Verlag, Berlin, 1972, pp. 470-483.

Danis, P. and Meur, G., Phenomenes de sommation dans l'amblyopie strabique, Doc. Ophthal. 23, 203-209, 1967.

Daw, N. W. and Enoch, J. M., Contrast sensitivity, Westheimer function and Stiles-Crawford effect in a blue cone monochromat, Vision Res. 13, 1669-1680, 1973.

Denton, E. J. and Nicol, J. A. C., The choroidal tapeta of some cartilaginous fishes, J. Marine Biol. Assoc. U. K. 44, 219-258, 1964.

Donner, K. O. and Rushton, W. A. J., Rod-cone interaction in the frog's retina analysed by the Stiles-Crawford effect and by dark adaptation, J. Physiol. 149, 303-317, 1959.

Drum, B., Additivity of the Stiles-Crawford effect for a Fraunhofer image, Vision Res. 15, 291-298, 1975.

Dunnewold, C. J. W., On the Campbell and Stiles-Crawford effects and their clinical importance, Soesterberg: The Institute for Perception, RVO-TNO, 1964.

Enoch, J. M., Amblyopia and the Stiles-Crawford effect, Amer. J. Optom. and Arch. Amer. Acad. Optom. 34, 298-309, 1957.

Enoch, J. M., Summated response of the retina to light entering different parts of the pupil, J. Opt. Soc. Amer. 48, 392-405, 1958.

Enoch, J. M., Receptor amblyopia, Amer. J. Ophthalmol. 48, 262-273, 1959a.

Enoch, J. M., Further studies on the relationship between amblyopia and the Stiles-Crawford effect, Amer. J. Optom. and Arch. Amer. Acad. Optom. 36, 111-128, 1959b.

Enoch, J. M., Optical interaction effects in models of parts of visual receptors, Arch. Ophthalmol. 63, 548-558, 1960.

Enoch, J. M., Nature of the transmission of energy in the retinal receptors, J. Opt. Soc. Amer. 51, 1122-1126, 1961a.

Enoch, J. M., Visualization of waveguide modes in retinal receptors, Amer. J. of Ophthalmol. 51, 1107-1118, 1961b.

Enoch, J. M., Waveguide modes in retinal receptors, Science 133, 1353-1354, 1961c.

Enoch, J. M., Optical properties of the retinal receptors, J. Opt. Soc. Amer. 53, 71-85, 1963.

Enoch, J. M., The current status of receptor amblyopia, Doc. Ophthal. 23, 130-148, 1967a.

Enoch, J. M., The retina as a fiber optics bundle, in Kapany, N. S., Fiber Optics, Principles and Applications, Academic Press, N. Y., 1967b, pp. 372-396.

Enoch, J. M., Retinal directional resolution in Pierce, J. and Levine, J. (eds.), Visual Science, Indiana Univ. Press, Bloomington, Ind., 1971.

Enoch, J. M., Retinal receptor orientation and the role of fiber optics in vision, Amer. J. Optom. and Arch. Amer. Acad. Optom. 49, 455-470, 1972.

Enoch, J. M., Effect of substantial accommocation on total retinal area, J. Opt. Soc. Amer. 63, 899, 1973.

Enoch, J. M., Vertebrate rod receptors are directionally sensitive, in Snyder, A. W. and Menzel, R. (eds.), Photoreceptor Optics, Springer Verlag, Berlin, 1975, pp. 17-37.

Enoch, J. M. and Bedell, H. E., Specification of the directionality of the Stiles-Crawford function, J. Opt. Soc. Amer., submitted, 1978.

Enoch, J. M., Bedell, H. E. and Campos, E. C., Local variations in rod receptor orientation, Vision Res. 18, 123-124, 1978.

Enoch, J. M. and Glismann, L. E., Physical and optical changes in excised retinal tissue, Invest. Ophthal. 5, 208-221, 1966.

Enoch, J. M. and Hope, G. M., An analysis of retinal receptor orientation III. Results of initial psychophysical tests, Invest. Ophthalmol. 11, 765-782, 1972a.

Enoch, J. M. and Hope, G. M., An analysis of retinal receptor orientation IV. Center of the entrance pupil and the center of convergence of orientation and directional sensitivity, Invest. Ophthalmol 11, 1017-1021, 1972b.

Enoch, J. M. and Hope, G. M., Directional sensitivity of the foveal and parafoveal retina, Invest. Ophthalmol. 12, 497-503, 1973.

Enoch, J. M. and Horowitz, B. R., The vertebrate retinal receptors as a waveguide in Proceedings of the Polytechnique Institute of New York Microwave Research Institute Symposium, Vol. 23, Polytechnic Press, N. Y., 1974, pp. 133-159.

Enoch, J. M. and Laties, A. M., An analysis of retinal receptor orientation II. Predictions for psychophysical tests, Invest. Ophthalmol. 10, 959-970, 1971.

Enoch, J. M. and Stiles, W. S., The colour change of monochromatic light with retinal angle of incidence, Optica Acta 8, 329-358, 1961.

Enoch, J. M. and Tobey, F. L., Special microscope microspectrophotometer: Optical design and application to the determination of waveguide properties of frog rods, Opt. Soc. Amer. 63, 1345-1356, 1973.

Enoch, J. M. and Tobey, F. L., Difference in the index of refraction between the rat rod outer segment and the interstitial matrix, J. Opt. Soc. Amer., in press, 1978.

Enoch, J. M., vanLoo, J. A. and Okun, E., Realignment of photoreceptors disturbed in orientation secondary to retinal detachment, Invest. Ophthalmol. 12, 849-853, 1973.

Ercoles, A. M., Ronchi, L. and Toraldo di Francia, G., The relation between pupil efficiencies for small and extended pupils of entry, Óptica Acta 3, 84-89, 1956.

Fankhauser, F. and Enoch, J. M., The effects of blur upon perimetric thresholds, Arch. Ophthalmol. 86, 240-251, 1962.

Fankhauser, F., Enoch, J. M. and Cibis, P., Receptor orientation in retinal pathology, Amer. J. Ophthalmol. 52, 767-783, 1961.

Fankhauser, F. and Röhler, R., The physical stimulus, the quality of the retinal image and foveal brightness discrimination in one amblyopic and two normal eyes, Doc. Ophthal. 23, 149-184, 1967.

Fitzgerald, C. R., Enoch, J. M., Campos, E. C. and Bedell, H. E., Comparison of visual function studies in two cases of senile macular degeneration, Klin. Monatsbl. f. Augenheilk., in press, 1978.

Flamant, F. and Stiles, W. S., The directional and spectral sensitivities of the retinal rods to adapting fields of different wavelengths, J. Physiol. 107, 187-202, 1948.

Flynn, J. T., Spatial summation in amblyopia, Arch. Ophthalmol. 78, 470-474, 1967.

Flynn, J. T., McKenney, S. G. and Dannheim, E., Brightness matching in strabismic amblyopia, Am. Orthoptic J. 21, 38-49, 1971.

Goldmann, H., Stiles-Crawford-Effekt, Ophthalmologica 103, 225-229, 1942.

Goodeve, C. F., Relative luminosity in the extreme red, Proc. Roy. Soc. Lond. A155, 664-683, 1936.

Green, D. G., Visual resolution when light enters the eye through different parts of the pupil, J. Physiol. 190, 583-593, 1967.

Gregory, R. L., Eye and Brain, McGraw-Hill, N. Y., 1973.

Grosvenor, T., The Effects of duration and background luminance upon the brightness discrimination of an amblyope, Am. J. Optom. and Arch. Amer. Acad. Optom. 34, 639-663, 1957.

Gstalder, R. J. and Green, D. G., Laser interferometric acuity in amblyopia, J. Ped. Ophthalmol. 8, 251-256, 1971.

Gullstrand, A., in von Helmholtz, H., Physiological Optics, Vol. I, 3rd Ed., Dover, N. Y., 1962, pp. 356-357.

Hays, W. L., Statistics for Psychologists, Holt, Rinehart and Winston, N. Y., 1963.

Heath, G. G., Directional sensitivity of retinal receptors, J. Opt. Soc. Amer. 60, 736, 1970.

Heath, G. and Walraven, P. L.. Receptor orientations in the central retina, J. Opt. Soc. Amer. 60, 733-734, 1970 (Abstract).

Helmholtz, H., Treatise on Physiological Optics, (J. P. C. Southall, ed.), The Optical Society of America, Menasha, Wi., 1924.

Hubel, D. H. and Wiesel, T. N., Functional architecture of macaque monkey visual cortex, Proc. Roy. Soc. Lond. B198, 1-59, 1977.

Ikeda, H. and Wright, M. J., Is amblyopia due to inappropriate stimulation of the "sustained" pathway during development?, Brit. J. Ophthalmol. 58, 165-173, 1974.

Ikeda, H. and Wright M. J., Properties of LGN cells in kittens reared with convergent squint: A neurophysiological demonstration of amblyopia, Exp. Brain Res. 25, 63-77, 1976.

Johnson, C. A. and Leibowitz, H. W., Practice, refractive error, and feedback as factors influencing peripheral motion thresholds, Perc. and Psychophys. 15, 276-280, 1974.

Julesz, B., Foundations of Cyclopean Perception, University of Chicago Press, Chicago, 1971.

Kandel, G. L. and Bedell, H. E., A precise method of measuring fixational eccentricity using the Maxwell spot centroid, Behav. Res. Meth. and Instrum. 4, 295-296, 1972.

Kandel, G. L. and Bedell, H. E., Peripheral acuity in strabismic amblyopes and normal observers, paper presented at Assoc. for Res. in Vision and Ophthalmol., May, 1973.

Kandel, G. L. and Bedell, H. E., Eccentricity of the scotopic fovea about a photopic point as revealed by acuity contours, Vision Res. 16, 357-362, 1976.

Kelly, D. H. and Savoie, R. E., A study of sine-wave contrast sensitivity by two psychophysical methods, Perc. and Psychophys. 14, 313-318, 1973.

King-Smith, P. E., The Stiles-Crawford effect and waveguide modes: An explanation of MacLeod's paradox in terms of local adaptation within outer segments, Vision Res. 14, 593-595, 1974.

Kirschen, D., Personal communication, 1977.

Laties, A. M., Histological techniques for study of photoreceptor orientation, Tissue and Cell 1, 63-81, 1969.

Laties, A. M. and Enoch, J. M., An analysis of retinal receptor orientation I. Angular relationship of neighboring photoreceptors. Invest. Ophthalmol. 10, 69-77, 1971.

Laties, A. M., Liebman, P. A. and Campbell, C. E. M., Photoreceptor orientation in the primate eye, Nature 218, 172-173, 1968.

Lawill, T., Meur, G. and Howard, C. W., Lateral inhibition in the central visual field of an amblyopic subject, Am. J. Ophthalmol. 76, 225-228, 1973.

LeGrand, Y., Recherches sur l'effet Stiles-Crawford, Revue d'Optique 16, 759, 1948.

LeGrand, Y., Light, Colour and Vision, Chapman and Hall, London, 1968, pp. 103-108.

Lemcke, H. H. and Pischel, D. K., Retinal detachments after the use of phospholine iodide, Trans. Pacific Coast Oto-Ophthalmol. Soc. 47, 157-163, 1966.

MacLeod, D. I. A., Directionally selective light adaptation: A visual consequence of receptor disarray?, Vision Res. 14, 369-378, 1974.

MacNichol, E. F., How to apply system analysis properly to biological systems, IEEE Int. Conv. Rec. 15, 212-228, 1967.

Makous, W. L., A transient Stiles-Crawford effect, Vision RES. 8, 1271-1284, 1968.

Makous W., Some functional properties of visual receptors and their optical implications, J. Opt. Soc. Amer. 67, 1362, 1977.

Mandelbaum, J. and Sloan, L. L., Peripheral visual acuity, Am. J. Ophthalmol. 30, 581-588, 1947.

Marshall, R. L. and Flom, M. C., Amblyopia, eccentric fixation and the Stiles-Crawford effect, Amer. J. Optom. and Arch. Amer. Acad. Optom 47, 81-90, 1970.

Mellerio, J., Light absorption and scatter in the human lens, Vision Res. 11, 129-141, 1971.

Meur, G. and Conreur, L., Contribution a l'étude de l'acuité visuelle peripherique chez le sujet normal et chez l'amblyope, Bull. Soc. Belge d'Ophthalmol. 150, 694-700, 1968.

Miller, N. D., The changes in the Stiles-Crawford effect with high luminance adapting fields, Amer. J. Optom. and Arch. Amer. Acad. Optom. 41, 599-608, 1964.

Moon, P. and Spencer, D. E., On the Stiles-Crawford effect, J. Opt. Soc. Amer. 34, 319-329, 1944.

Moses, R., Adler's Physiology of the Eye, Mosby, St. Louis, 1970.

Nicol, J. A. C., The tapetum lucidum of the sturgeon, Contrib. in Marine Sci. 14, 5-18, 1969.

Norton, T. T., Casagrande, V. A. and Sherman, S. M., Loss of Y-cells in the lateral geniculate nucleus of monocularly deprived tree shrews, Science 197, 784-786, 1977.

O'Brien, B., A theory of the Stiles and Crawford effect, J. Opt. Soc. Amer. 36, 506-509, 1946.

O'Brien, B., Local variations of the Stiles and Crawford effect, J. Opt. Soc. Amer. 40, 796, 1950.

O'Brien, B., Vision and resolution in the central retina, J. Opt. Soc. Amer. 41, 882-894, 1951.

Ogle, K., Foveal contrast thresholds with blurring of the retinal image and increasing size of test stimulus, J. Opt. Soc. Amer. 51, 862-869, 1961a.

Ogle, K., Peripheral contrast thresholds and blurring of the retinal image for a point light source, J. Opt. Soc. Amer. 51, 1265-1268, 1961b.

Ohzu, H. and Enoch, J. M., Optical modulation by the isolated human fovea, Vision Res. 12, 245-251, 1972.

Ohzu, H., Enoch, J. M. and O'Hair, J. C., Optical modulation by the isolated retina and retinal receptors, Vision Res. 12, 231-244, 1972.

Pask, C. and Snyder, A. W., Theory of the Stiles-Crawford effect of the second kind, in Snyder, A. A. and Menzel, R. (eds.), Photoreceptor Optics, Springer-Verlag, Berlin, 1975, pp. 145-158.

Pautler, E. L., Directional sensitivity of isolated turtle retinas, J. Opt. Soc. Amer. 57, 1267-1269, 1967.

Pokorny, J., Smith, V. C., Diddie, K. R., Newell, F. and Mausolf, F., Color matching and Stiles-Crawford effect in early senile macular degeneration-pilot data, presented at Assoc. for Res. in Vision and Ophthalmol., May, 1977.

Richards, W., Saccadic suppression, J. Opt. Soc. Amer. 59. 617-623, 1969.

Riggs, L. A., Light as a stimulus for vision, in Graham, C. H. (ed.), Vision and Visual Perception, Wiley and Sons, N. Y., 1965, pp. 1-38.

Ripps, H. and Weale, R. A., Photo-labile changes and the directional sensitivity of the human fovea, J. Physiol. 173, 57-64, 1964.

Rodieck, R. W., The Vertebrate Retina, Principles of Structure and Function, W. H. Freeman, San Francisco, 1973.

Ronchi, L., Influenza di un midriatico sull'effetto Stiles-Crawford, Atti Della Fond. G. Ronchi 9, 394-399, 1954.

Ronchi, L., On the influence of mydriatics and miotics on visual functions, Atti Della Fond. G. Ronchi 10, 285-308, 1955.

Rushton, W. A. H., Visual pigments in man, in Dartnall, H. J. A. (ed.), Photochemistry of Vision, Handbook of Sensory Physiology, Vol. VII/1, Springer-Verlag, Berlin, 1972, pp. 364-394.

Safir, A. and Hyams, L., Distribution of cone orientations as an explanation of the Stiles-Crawford effect, J. Opt. Soc. Amer. 59, 757-765, 1969.

Safir, A., Hyams, L. and Philpot, J., Movement of the Stiles-Crawford effect, Invest. Ophthalmol. 9, 820-825, 1970.

Safir, A., Hyams, L. and Philpot, J., The retinal directional effect: A model based on the Gaussian distribution of cone orientations, Vision Res. 11, 819-831, 1971.

Sandberg, M. A., The origin and control of eccentric fixation in amblyopia, Ph.D. Dissertation, Brown University, 1974.

Sansbury, R., Zacks, J. and Nachmias, J., The Stiles-Crawford effect: Two models evaluated, Vision Res. 14, 803-812, 1974.

Schlaer, S., The relation between visual acuity and illumination, J. Gen. Physiol. 21, 165-188, 1937.

Sherman, S. M., Hoffmann, K. P and Stone, J., Loss of a specific cell type from dorsal lateral geniculate nucleus in visually deprived cats, J. Neurophysiol. 35, 532-541, 1972.

Sidman, R. L., The structure and concentration of solids in photoreceptor cells studied by refractometry and interference microscopy, J. of Biophys. and Biochem. Cytol. 3, 15-30, 1957.

Siegel, S., Nonparametric Statistics for the Behavioral Sciences, MaGraw-Hill, N. Y., 1956.

Simon, R., "Über Fixation im Dammerungssehen, Zeitschrift für Psychologie 36, 186-193, 1904.

Smith, V. C., Pokorny, J. and Ernest, J. T., Visual function in acuite posterior multifocal placoid pigment epitheliopathy, presented at Assoc. for Res. in Vision and Ophthalmol., May, 1977.

Snyder, A. W. and Hamer, M., The light capture area of a photoreceptor, Vision Res. 12, 1749-1753, 1972.

Snyder, A. W. and Menzel, R. (eds.), Photoreceptor Optics, Springer-Verlag, Berlin, 1975.

Snyder, A. W. and Pask, C., The Stiles-Crawford effect - explanation and consequences, Vision Res. 13, 1115-1137, 1973.

Spring, K. H. and Stiles, W. S., Variation of pupil size with change in the angle at which the light stimulus strikes the retina, Brit. J. Ophthalmol. 32, 340-346, 1948.

Sternheim, C. E. and Riggs, L. A., Utilization of the Stiles-Crawford effect in the investigation of the origin of the electrical responses of the human eye, Vision Res. 8, 25-33, 1968.

Stiles, W. S., The luminous efficiency of monochromatic rays entering the eye pupil at different points and a new colour effect, Proc. Roy. Soc. Lond. B123, 90-118, 1937.

Stiles, W. S., The directional sensitivity of the retina and the spectral sensitivities of the rods and cones, Proc. Roy. Soc. Lond. B127, 64-105, 1939.

Stiles, W. S., Personal communication to Jay Enoch, 1959.

Stiles, W. S., The directional sensitivity of the retina, Ann. Roy. Coll. Surgeons. Eng. 30, 73-101, 1962.

Stiles, W. S. and Crawford, B. H., The luminous efficiency of rays entering the eye pupil at different points, Proc. Roy. Soc. Lond. B112, 428-450, 1933.

Tansley, K. and Johnson, B. K., The cones of the grass snake's eye, Nature 178, 1285-1286, 1956.

Toraldo di Francia, G., Retina cones as dielectric antennas, J. Opt. Soc. Amer. 39, 324, 1949.

Tobey, F. L., Enoch, J. M. and Scandrett, J. H., Experimentally determined optical properties of goldfish's cones and rods, Invest. Ophthal. 14, 7-23, 1975.

vanLoo, J. A. and Enoch, J. M., The Scotopic Stiles-Crawford effect, Vision Res. 15, 1005-1009, 1975.

Viefhues, T. K. and Kühnhardt, G., Die objective Prüfung der Sehschärfe bei Schielamblyopie, v. Graefes Archiv. f. Ophthalmol. 160, 263-266, 1958.

von Noorden, G. K., The pathogenesis of eccentric fixation, Am. J. Ophthalmol. 61, 399-422, 1966.

von Noorden, G. K. and Crawford, M. L. J., Form deprivation without light deprivation produces the visual deprivation syndrome in macaca mulatta, Brain Res. 129, 37-44, 1977.

Vos, J. J., Some new aspects of color stereoscopy, J. Opt. Soc. Amer. 50, 785-790, 1960.

Vos, J. J., The color stereoscopic effect, Vision Res. 6, 105-107, 1966.

Vos, J. J. and Huigen, A., A clinical Stiles-Crawford apparatus, Amer. J. Optom. and Arch. Amer. Acad. Optom. 39, 68-76, 1962.

Vos, J. J. and van Os, F. L., The effect of lens density on the Stiles-Crawford effect, Vision Res. 15, 749-751, 1975.

Walraven, P. L., Recovery from the increase of the Stiles-Crawford effect after bleaching, Nature 210, 311-312, 1966.

Walraven, P. L. and Bouman, M. A., Relation between directional sensitivity and spectral response curves in human cone vision, J. Opt. Soc. Amer. 50, 780 - 784, 1960.

Walraven, P. L. and Leebeck, H. J., Chromatic Stiles-Crawford effect of anomalous trichromats, J. Opt. Soc. Amer. 52, 836-837, 1962.

Weale, R. A., Notes on the photometric significance of the human crystalline lens, Vision Res. 1, 183-191, 1961.

Webb, N. G., X-ray diffraction from outer segments of visual cells in intact eyes of the frog, Nature 235, 44-46, 1972.

Webb, N. G., Orientation of retinal rod photoreceptor membranes in the intact eye using X-ray diffraction, Vision Res. 17, 625-631, 1977.

Westheimer, G., The Maxwellian view, Vision Res. 6, 669-682, 1966.

Westheimer, G., Dependence of the magnitude of the Stiles-Crawford effect on retinal location, J. Physiol. 192, 309-315, 1967.

Westheimer, G., Entoptic visualization of Stiles-Crawford effect, Arch. Ophthalmol. 79, 584-588, 1968.

Wiesel, T. N. and Hubel, D. H., Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body, J. Neurophysiol. 26, 978-995, 1963a.

Wiesel, T. N. and Hubel, D. H., Single-cell responses in striate cortex of kittens deprived of vision in one eye, J. Neurophysiol. 26, 1003-1017, 1963b.

Wijngaard, W., Bouman, M. A., and Budding, F., The Stiles-Crawford colour change, Vision Res. 14, 951-957, 1974.

Wijngaard, W. and van Kruysbergen, J., The function of the non-guided light in some explanations of the Stiles-Crawford effects, in Snyder, A. W. and Menzel, R. (eds.), Photoreceptor Optics, Springer-Verlag, Berlin, 1975, pp. 175-183.

Wilcox, W. W., The basis of the dependence of visual acuity on illumination, Proc. Nat. Acad. Sci. 18, 47-56, 1932.

Williams, E. J., Regression Analysis, Wiley and Sons, N. Y., 1959.

Wooten, B. R., Fuld, K., Katz, L. and Moore, M., The Stiles-Crawford II effect at high bleaching levels, J. Opt. Soc. Amer. 67, 1362, 1977.

Wright, W. D., Researches on Normal and Defective Colour Vision, Kimpton, London, 1946, pp. 88-95.

Wright, W. D. and Nelson, J. H., The relation between the apparent intensity of a beam of light and the angle at which the beam strikes the retina, Proc. Phys. Soc. Lond. 48, 401-405, 1936.

Wyszecki, G. and Stiles, W. S., Color Science, Wiley and Sons, N. Y., 1967, pp. 561-564.

Young, R., Visual cells and the concept of renewal, Invest. Ophthalmol. 15, 700-725, 1976.

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